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Comparative ecology of two sympatric species of atherinids, Menidia menidia and Membras martinica

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COMPARATIVE ECOLOGY OF TWO SYMPATRIC SPECIES OF ATHERINIDS, *MENIDIA MENIDIA* AND *MEMBRAS MARTINICA*

A Thesis

Presented to

The Faculty of the School of Marine Science

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Master of Arts

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William H. Burton

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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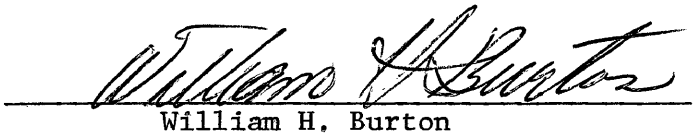

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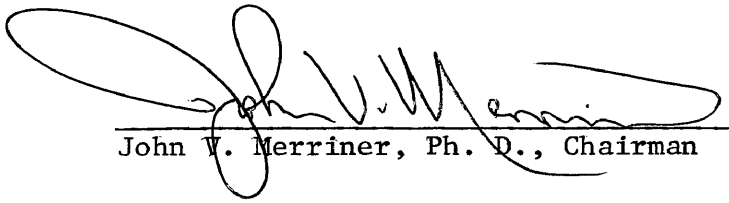
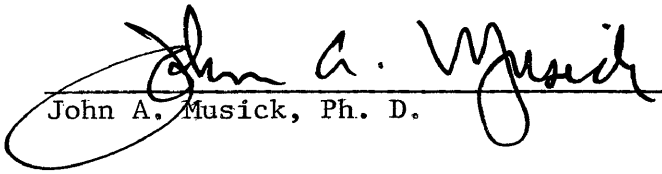


John V. Merriner, Ph. D., Chairman



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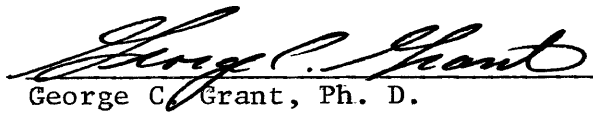

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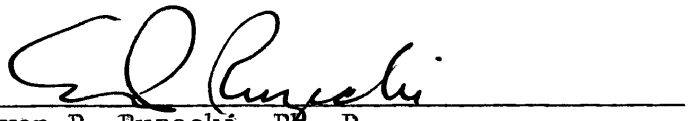
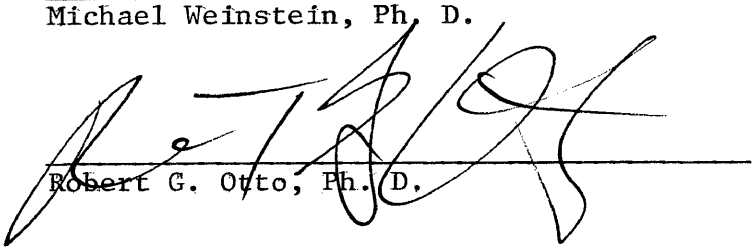


Evon P. Ruzecki, Ph. D.

Michael Weinstein, Ph. D.



Robert G. Otto, Ph. D.

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I wish to thank Dr. John Merriner for his careful review of the manuscript and encouragement with the original proposal. Thanks are also extended to Drs. Jack Musick, George Grant, John Ruzecki, Michael Weinstein and Robert Otto for serving as committee members and offering useful suggestions. A special thanks to Dr. George Grant for providing lab space and data from his lower bay survey. John Olney's and Tom Munroe's direction and keen interest in this research is gratefully appreciated. Regards to Dr. Joseph Loesch for his patience during my frequent questions about statistics. Thanks are extended to Robert Dias and Frank Wojcik for their assistance with my computer problems, and to Mary Ann Foell for drafting most of the figures. This study was partially funded by Sigma Xi, The Scientific Research Society and a Mini-Grant from the College of William and Mary.

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ABSTRACT

The trophic interactions, spatial and temporal distributions of Menidia menidia and Membras martinica in the lower Chesapeake Bay were determined through feeding and vertical distribution experiments, gut content analyses, neuston collections, and beach seining techniques. Feeding experiments and gut content and analyses indicated that Menidia > 61 mm ate epibenthic prey and zooplankton, while Membras fed exclusively on zooplankton. Membras adults and juveniles were abundant in surface mid-bay waters. Menidia never occurred offshore, but concentrated in shallow inshore zones at or near the bottom. Membras juveniles > 5 mm occurred in large numbers offshore from June through August, 1981. Mid-bay surface waters are believed to be an important nursery area for juvenile Membras. Juvenile Menidia were absent mid-bay, and appear to inhabit inshore environments. Membras catches were much greater in the James than in the York or the Rappahannock drainages. Menidia and Membras were found to be ecologically separated with respect to food selection, vertical and geographic distribution, and salinity preference.

Comparative Ecology of two Sympatric Atherinids, *Membras martinica* and *Menidia menidia*.

INTRODUCTION

The competitive exclusion principle states that "complete competitors cannot coexist" (Gause 1934). In theory, sympatric species that occupy a similar niche and compete for limited resources will eventually adapt to avoid competition with each other or one will become extinct. Niches may be partitioned spatially (by occupying different habitats), temporally (by occupying an area at different times of the day or season), or by utilizing different food resources (Schoener 1974). Also, similarity between species in one niche dimension (i.e. food) can be compensated by a dissimilarity in some other niche dimension (i.e. habitat) (Schoener 1974). Partitioning resources reduces niche overlap, and hence competition with other species (Mayr 1942, Yoshiyama 1980). With less interspecific interferences, a species is better able to find food, shelter, and ultimately a mate, thus insuring species survival. However, the existence of non-overlap in resource dimensions does not necessarily indicate that the observed partitioning was a result of competition for limited resources by coevolving species. The species could have evolved separately, and later become sympatric (Connell 1980). To state that coevolution has taken place, one would have to demonstrate that the species were sympatric during their evolutionary divergence, that they were in competition for similar resources, and that the divergence has a genetic basis (Connell 1980).

Regardless of the difficulties with explanations about the evolutionary mechanisms of resource partitioning, studies on such matters can provide valuable insight into the relationships between extant sympatric species, which may uncover important clues to their evolutionary past. Furthermore, information on interspecific relationships is needed to understand community structure, predator-prey interactions, and general ecological principles.

Membras martinica (Valenciennes) and Menidia menidia (Linnaeus) (Family Atherinidae) are zooplanktivorous fishes found in the lower Chesapeake Bay from May through December (Hildebrand and Schroeder 1928; Martin and Drewry 1978). They differ morphologically in their scale types (cycloid in Menidia/ctenoid in Membras) and pigmentation (Menidia has tiny melanophores bordering the edges of its scales, and Membras has larger melanophores and longitudinal rows anterior to the scale edges). The two species are somewhat separated geographically in that Membras martinica ocurs more frequently at higher salinities in the southern portion of the bay, whereas Menidia menidia is distributed widely throughout the bay (Hildebrand and Schroeder 1928; Martin and Drewry 1978).

Spawning in the Atlantic silverside (Menidia menidia) and in the rough Silverside (Membras martinica) occurs in early spring in similar inshore habitats (Martin and Drewry 1978). Menidia menidia has been reported to spawn as early as April in the Beaufort, North Carolina area (Moore 1980), and in Maryland waters (Nichols 1908). In Virginia, the earliest known spawning by Menidia was in May (Fowler

1918; as cited by Martin and Drewry 1978). Ripe female Membras occur in May to late July or early August in the Chesapeake and North Carolina region (Hildebrand and Schroeder 1928; Kuntz 1916; Martin and Drewry 1978; Rubbinoff 1961). Both species spawn in salinities less than 15 °/oo (Polgar et al. 1979), and both Menidia (Bayliff 1950) and Membras (Martin and Drewry 1978) possess a protracted spawning period.

Where these species overwinter is not exactly known, especially in the case of Membras, but there are reports that Membras leave the Chesapeake Bay for offshore areas at the onset of lower temperatures (Gunter 1945, Conover and Murawski in press). Bayliff (1950) reported that in the Chesapeake, Menidia menidia remain year round and overwinter in deep water. In addition, the Atlantic silversides have been noted to occur through the winter in deep mid-marsh channels at Virginia's seaside waters (Richards and Castagna 1970).

Membras martinica is frequently found along open nonvegetated beaches where the bottom consists of hard sand or mud (Robins 1969; Gunter 1945). Menidia menidia is also commonly found along open beaches, but with sand or gravel bottom types (Robins 1969).

Little has been published on the diet of Membras martinica. Reid (1954) and Hildebrand and Schroeder (1928) found that their diet consisted mainly of copepods and insects caught at the surface. Menidia menidia was reported to feed on copepods, amphipods, annelids, and mysids (Gilmurray and Daborn 1981; Linton 1901, as cited by Robins 1969; Robins 1969). Harpacticoids were found to be important in the diets of 10-30 mm Menidia menidia (Mulkana 1966).

Menidia menidia and Membras martinica can be found together in midsummer beach siene hauls in the southern portion of the Chesapeake Bay (pesonal observation). How these species interact with each other in terms of habitat, time, and food resources is a relevant problem in contemporary ecology, which provides an opportunity to apply and test current ecological models and theories.

This study compares the food and habitat preferences of these species and determines the degree of niche overlap and resource partitioning that may occur between them.

Based upon results from a preliminary field assessment of diet in Menidia and Membras (see Appendix A), I decided to evaluate the feeding relationships of these fishes under controlled laboratory conditions. An experimental approach was used in the present study because stomach content analyses of field collected fishes are often difficult to interpret in terms of selectivity (O'Brien and Vinyard 1974). In field studies the density and species composition of prey cannot be accurately assessed, and exactly where and when the predator last fed is unknown. Without precise knowledge of the prey community structure it would be difficult to distinguish between active food selection and opportunistic feeding.

By experimentally presenting Menidia menidia and Membras martinica with various concentrations and species of prey under controlled laboratory conditions, it was hoped that their trophic relationships and selectivity could be quantitatively assessed.

MATERIALS AND METHODS

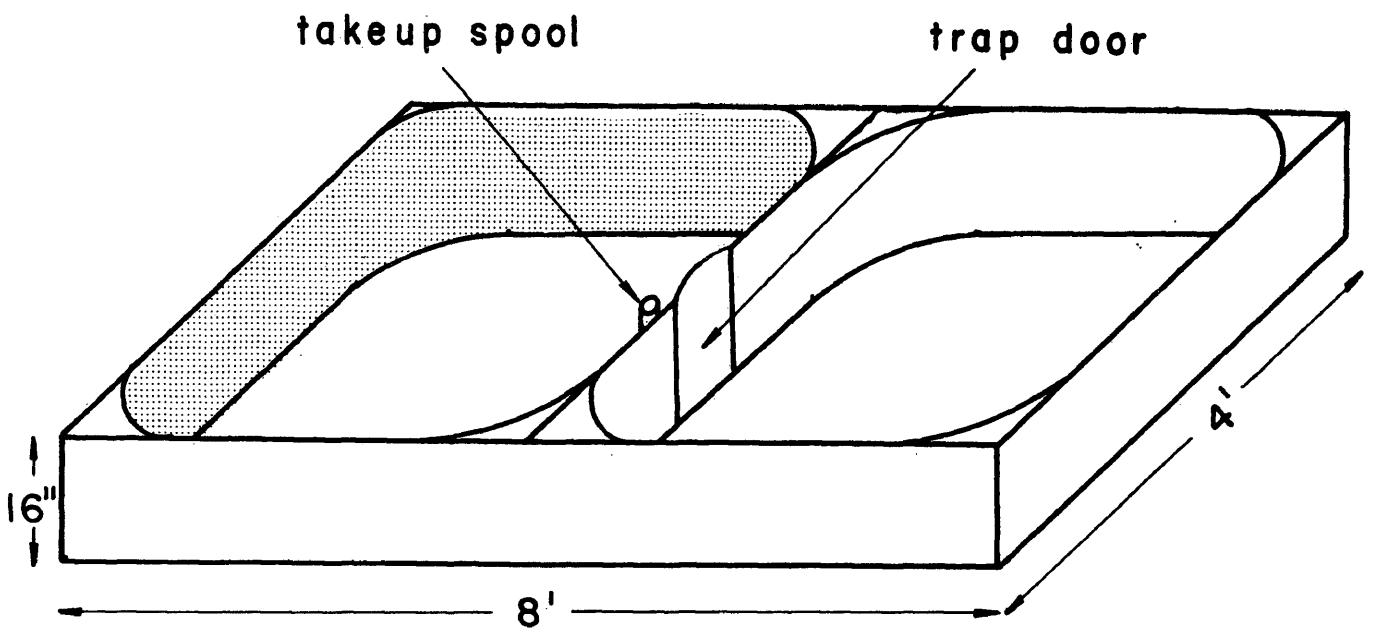
I. Feeding Experiments

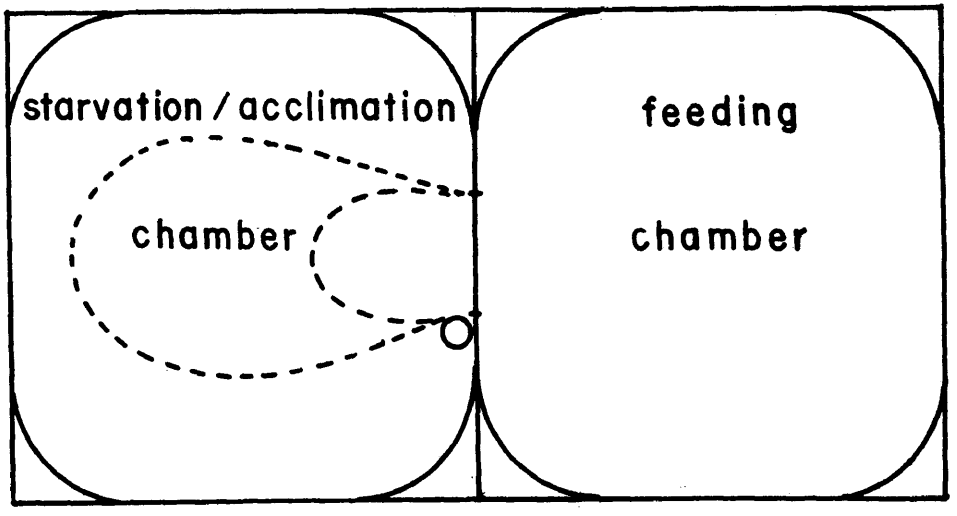
A) Experimental Chamber

An 8' x 4' x 16" tank was divided to form two compartments connected by a trap door. The tank was built of 3/4" plywood, reinforced with 2" x 2" braces and sealed with fiberglass tape. Sheets of curved plywood were attached to the corners to round them off (figure 1). The entire inside surface was coated with light green epoxy resin. Each chamber had an inside diameter of 44" and a 16" height; both were lighted by two 40 watt fluorescent lights. One was the starvation and acclimation chamber, which was kept free of any food items. The other was the feeding chamber, where live prey items were introduced over a 1" sand substrate. Live fishes were placed in the acclimation chamber 24 hours prior to each experiment to allow for gut clearance. The feeding chamber contained known quantities of epibenthic and zooplanktonic organisms.

To minimize disorientation and abnormal behavior that would occur if the fish were handled excessively, a device was installed to herd the fish from the starvation chamber to the feeding chamber. The herding device consisted of 1 mm x 1 mm plastic mesh screening attached at one end to the inside vertical edge of the doorway leading to the feeding chamber and at the other end to a take up spool placed

Figure 1. Experimental tank, showing the operation of the herding device.


takeup spool
trap door
16"
8'
4'


starvation / acclimation
chamber
feeding
chamber

on the opposite side of the doorway. In the opened position, the screening stood vertically around the perimeter of the tank. By rotating the take up spool, the tank's diameter decreased and the screening herded the test fishes toward the closed trap door. When they were concentrated near the door, it was opened momentarily to allow the fishes to enter the feeding chamber.

B) Plankton

The zooplankton used for the experiments were caught by fishing the tide from a pier with a 76 µm plankton net and concentrated into a ten liter collection. From the original ten liter sample, three thoroughly mixed subsamples were removed, fixed, and examined under a dark field dissecting microscope for enumeration and species indentification. To facilitate ease of counting in a gridded petri dish, the volume of the replicate subsamples varied for each experiment (the subsample volume was usually 10 ml).

Preliminary experiments, showed that polychaete larvae, Polydora sp., quickly dissolved when ingested by the fish thus they were indistinguishable for gut content analysis. Since Polydora sp. dominated daytime subsurface zooplankton collections, all subsequent live zooplankton samples for the feeding experiments were taken before dawn.

Depending upon the density of prey called for in a particular experiment and the calculated density of prey items in the 10 liter zooplankton collection, either all or a percentage of the original collection was used. Minutes prior to the start of an experiment, the

prescribed volume was gently sieved through a 60 μm nitex screen. The retained organisms were then quickly transferred to the feeding chamber.

C) Epibenthic organisms

The epibenthic prey were collected from traps placed on the bottom by the VIMS pier where the zooplankton was collected. The traps consisted of 2' x 8" chicken wire cylinders stuffed with 1 mm x 1 mm plastic mesh screening. The traps were retrieved several hours prior to each experiment, and the organisms clinging to the mesh were rinsed off into a cooler. With a 202 μm nitex sieve, the retained organisms were transferred to a 5 liter bucket and returned to the lab for counting. From the 5 liter collection, three thoroughly mixed 30 ml subsamples were removed and analyzed as described above for zooplankton. As with the zooplanktonic organisms, either all or a percentage of the original 5 liter collection was gently sieved and transferred to the feeding chamber.

D) Prey species proportions and densities

Based on the subsample counts, the number of prey per ml in both the zooplankton and epibenthic collections was calculated by dividing the sum of the mean counts for all species ($\Sigma \bar{X}$ zoo. and $\Sigma\bar{X}$ epi., respectively) by the subsample volume (sub. ml). The total number of prey in each collection was estimated by multiplying the calculated numbers of prey per ml by the collection volume. Since the volume of the feeding chamber was known (348 liters) the number of zooplankton to be placed in the chamber that would approximate natural densities

was derived (≈60 per liter). Similarly, the area of the substrate was known, and the numbers of epibenthic prey needed to obtain a density of ≈5 prey per 10 cm^2 was calculated. Thus, the percentage of each prey collection to be transferred to the feeding chamber was determined.

Since the zooplankton and epibenthic organisms were mixed together in the feeding chamber, the species proportions changed relative to the original collections. To account for this, the coefficents f_1 and f_2 were generated and applied to the counts of each species in each replicate subsample of the zooplankton and epibenthic collections respectively, defined as

$$f_2 = \frac{\frac{\Sigma\bar{X}_{epi.}}{\text{sub. mls}} \times \text{Volume Filtered (epi.)}}{\frac{\Sigma\bar{X}_{zoo.}}{\text{sub. mls}} \times \text{Volume Filtered (zoo.)}}$$

and

$$f_1 = 1 - f_2$$

where f_1 corresponds to the zooplankton counts and f_2 to the epibenthic counts.

E) Fish

The fishes were held in a closed brackish water system under ambient salinities and temperatures with a photoperiod of twelve hours light and twelve hours dark. A large 20' x 4' deep wading pool served as the reservoir for the system. Water was constantly circulated from

the reservoir to a biological filter and distributed to the holding tanks. The water used for each experiment was filtered with a 15 µm filter bag as it was pumped from the reservoir to the experimental tank. Replacement water to the reservoir was pumped from the York River and filtered in the same manner.

The silversides were usually held for at least two weeks prior to experimentation. During acclimation, they were fed commercial flake food. Several preliminary experiments failed (i.e. the fishes did not eat live prey) since the fishes had become accustomed to flake food. Therefore prior to all reported experiments, the silversides were held in a 50 gallon aquarium for several days and fed a mixture of zooplankton and epibenthic prey from the York River. After this reacclimation to live food, the fishes were transferred to the starvation tank for 24 hours. Test fish were then moved into the feeding chamber via the herding device approximately ten minutes after the placement of live prey, and allowed to feed for five hours. A five hour feeding period was chosen because test fishes did not feed immediately when moved to the feeding chamber. Feeding usually started an hour or more after their introduction to the chamber. At the end of the feeding period, the fishes were removed and immediately preserved in 10% formalin for gut content analysis.

The stomach of each individual was dissected from the esophagus to the pylorus. The contents were rinsed into a gridded petri dish, and all prey species were counted. When the number of prey in the stomach was on the order of thousands, the contents were diluted

(usually to 80 mls) and three thoroughly mixed subsamples were counted.

F) Statistics:

Analysis of the experimental results of prey selection was partially accomplished through the use of Strauss's (1979) linear index of electivity L_i, defined as

$$L_i = r_i - p_i$$

where r_i is the proportion of species i in the ration and p_i is the proportion of species i in the environment. The index ranges from -1 to +1. Positive values indicate selection, negative values indicate avoidance or inaccessibility, and zero values are obtained if random selection occurs.

The selection index for each prey species was tested for significance from L=0 with Fleiss' (1981) Comparison of m Proportions chi square test

$$\chi^2 = \frac{1}{\bar{p}\bar{q}} \times \frac{n_1 \, n_2}{n..} \times (\bar{p}_2 - \bar{p}_1)^2$$

where n_1 is the total number of prey counted in the replicate subsamples of the environment; n_2 is the total number of prey counted in the stomachs of the fishes, and

$$n.. = n_1 + n_2$$

and

$$\bar{p}_1 = \frac{n_p}{n_1} = p_i$$

and

$$\bar{p}_2 = \frac{n_r}{n_2} = r_i$$

where n_p is the total number of species i counted from the subsamples of the environment; n_r is the total number of species i counted in the stomachs of the fishes, and

$$\bar{p}_2 - \bar{p}_1 = L_i$$

and

$$\bar{p} = \frac{n_p + n_r}{n..}$$

and

$$1 - \bar{p} = \bar{q}$$

The values of chi square were referred to the critical value with m -1 degrees of freedom, where m is equal to the numbers of subsamples of the environment plus the number of fishes in the comparison.

II. Vertical Distribution

Vertical distribution of Menidia menidia and Membras martinica in the water column was investigated through lab experiments and special field sampling.

A) Lab Experiment

A plexiglas frame (40 cm x 40 cm) was constructed and gridded off horizontally in 10 cm increments with colored string. The grid was divided in half by another string transecting it vertically. The frame was then submerged into a 50 gallon aquarium with the fishes and placed upright in the center of the tank. The tank was lighted with two 40 watt fluorescent lights suspended two feet above the tank. A

plastic tent was placed in front of the tank with a centered observation window.

Ample quantities of zooplanktonic and epibenthic prey items were placed in the tank 15 minutes prior to each experiment. Every 60 seconds the location of each individual fish on the grid was recorded with a mark on scaled graph paper. Only the fishes that were framed by the grid at the moment of observation were recorded. To observe night distributions, a red fluorescent light 6 feet away from the experimental area was momentarily switched on during each observation. No startle response was noted. Six Menidia and six Membras were used for the mixed species daylight experiment. Nine Menidia were used for the day versus night single species test, and 8 fishes were used in the Membras single species test.

B) Special Field Sampling

Vertical distribution of Membras in the field was defined using a weighted aluminum rectangular frame (0.5 x 1 meters) fitted with a 333 μm nitex net and flow meter.

During VIMS Planktology Department's lower bay zooplankton survey in October 1981, the rectangular frame was fished at three discrete depths, 0-0.5 meters, 1-1.5 meters, and 1.5-2 meters. All tows were done at night; each tow was of 10 minutes duration. The constraints of the survey schedule necessitated sampling of each discrete depth at different locations. These special samples were made when concurrent neuston (surface layer) collections indicated high densities of Membras in the area. The vessel was stationary as the net was

deployed and retrieved. While underway cable was let out to keep the net fishing at the prescribed depth. Samples were preserved and labelled for later analysis in the laboratory.

III. Inshore survey

Inshore distribution of Menidia menidia and Membras martinica was defined through the 1980 and 1981 striped bass seine survey (Burton and Dias 1981, Richards, et al. 1980). All samples were taken during daylight hours in both surveys. In the 1980 survey, field sampling was conducted tri-weekly from July 1 through October 24, 1980. Thirty fixed sampling stations (figure 2) were visited in each of five sampling periods. On each sampling date, the first station to be sampled was determined by random draw; additional stations convenient to the first station were then sampled. This process continued until all stations had been sampled. Most stations were sampled with a 90' x 4' x 1/4" mesh straight seine; usually one seine sweep was done at each station.

The 1981 survey included twenty eight stations sampled in each of four monthly periods from July 7 to November 6. Replicate sweeps were taken at each station. The sampling stations were the same as in 1980, with the exception of a few additions and deletions (figure 3). All stations were sampled with a 90' x 6' x 1/4" mesh seine with a collection bag.

All atherinids collected were identified to species and enumerated. Up to 25 specimens for each species were measured to the nearest mm fork length. Randomly chosen subsamples were preserved in

Figure 2. 1980 Juvenile striped bass survey sampling stations.

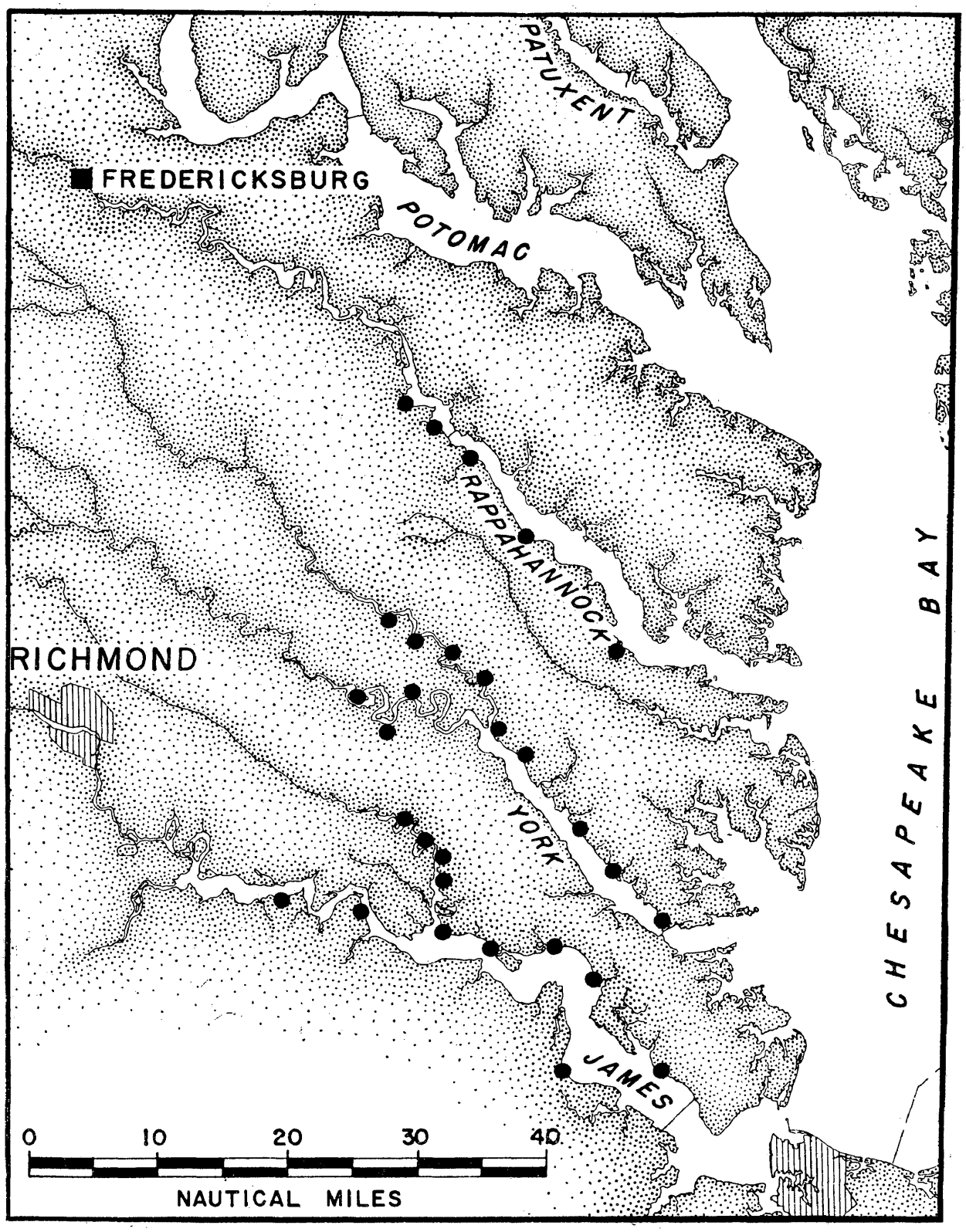
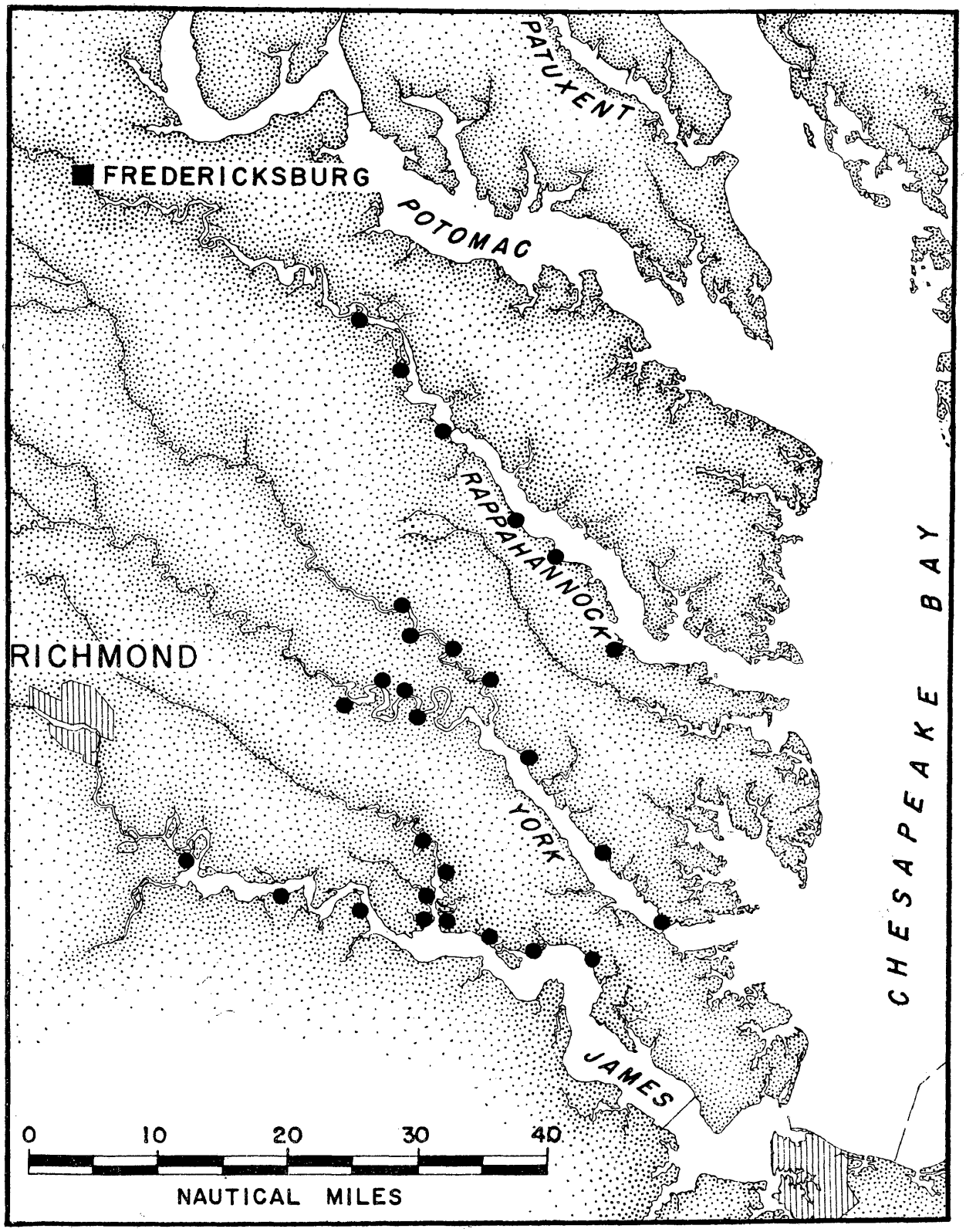

PATUXENT
FREDERICKSBURG
POTOMAC
RAPPAHANNOCK
RICHMOND
YORK
JAMES
CHESAPEAKE BAY
0
10
20
30
40
NAUTICAL MILES

Figure 3. 1981 Juvenile striped bass survey sampling stations.


PATUXENT
FREDERICKSBURG
POTOMAC
RAPPAHANNOCK
RICHMOND
YORK
JAMES
CHESAPEAKE BAY
0
10
20
30
40
NAUTICAL MILES

10% formalin on site and retained for future gut content analyses. Prior to each sampling, spatial, temporal, and physiochemical data were recorded which included location, time, water and air temperature, salinity, dissolved oxygen, tide stage, weather, wind direction and velocity.

IV. Offshore Survey

The spatial and temporal distribution of Membras in the open waters of the lower Chesapeake Bay was assessed through data collected from the 1978-1981 "Lower Bay Zooplankton Monitoring Program", initiated and directed by Dr. George Grant (VIMS). The 1981 survey was chosen for detailed analyses since sampling for that year covered the widest seasonal range.

Station locations were chosen randomly from a grid of stations (figure 4). On the average, 14 stations were sampled per cruise with effort divided into day and night stations (table 1).

A metered 100 cm x 35 cm deep neuston net (333 μm) was towed for approximately ten minutes at each station. The gear fished from surface to 12 cm depth. Data were expressed as square meters sampled for each tow. Prior to sampling, ancillary station data were taken such as, water temperature, salinity and dissolved oxygen (at 2 meter depth intervals), time, depth, tide and weather.

All adult fishes and larvae (including zooplankton) were preserved onboard and stored for later analyses. The samples were carefully sorted for adult, juvenile, and larval atherinids. Each

Figure 4. Chesapeake Bay sampling grid system used in lower bay zooplankton monitoring program.

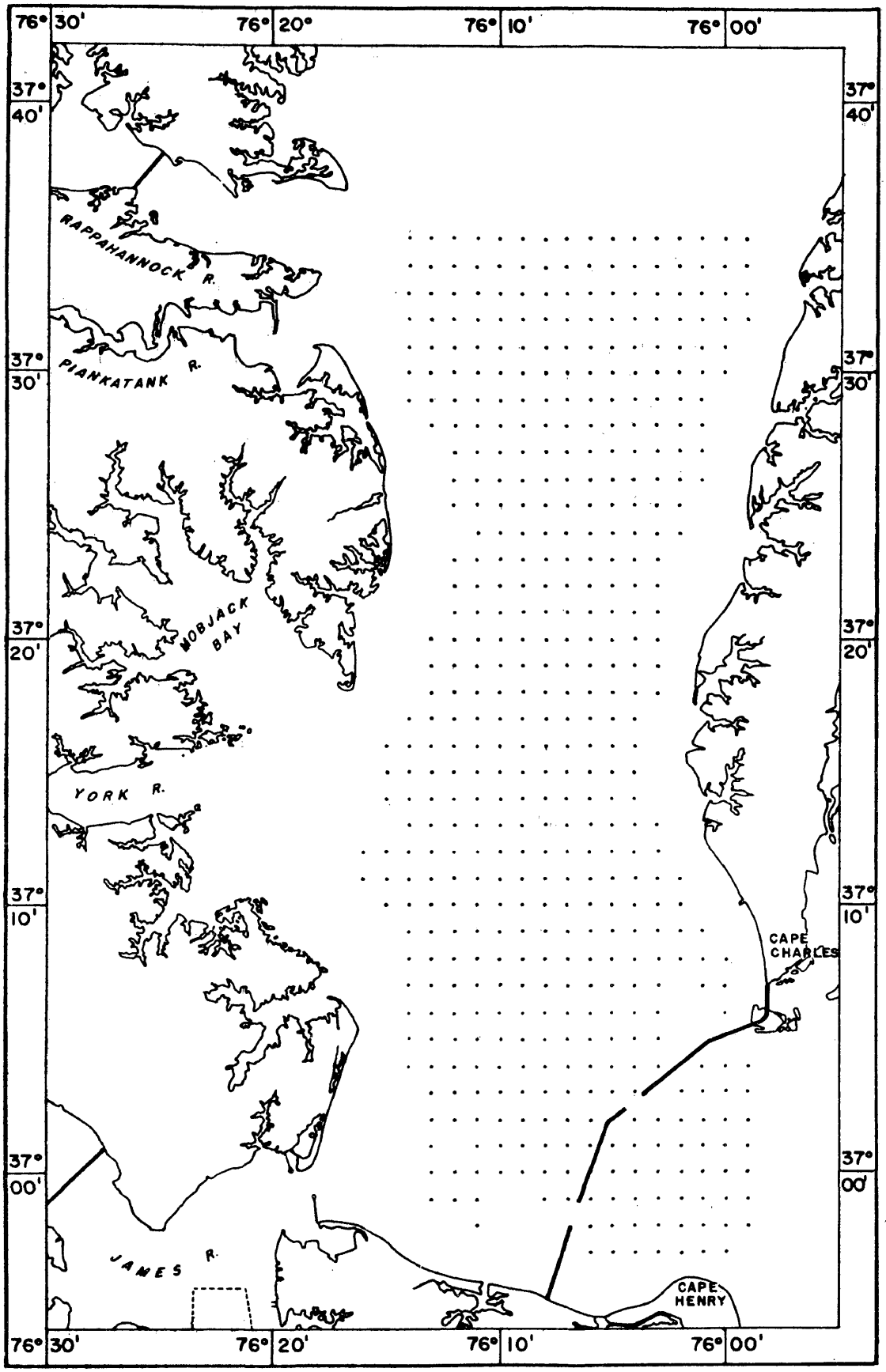

76° 30'
76° 20'
76° 10'
76° 00'
37° 40'
37° 30'
37° 20'
37° 10'
37° 00'
RAPPAHANNOCK R.
PIANKATANK R.
MOBJACK BAY
YORK R.
JAMES R.
CAPE CHARLES
CAPE HENRY

Table 1. 1981 Lower Bay Zooplankton Monitoring Effort.

Month	Total Stations	Day Stations	Night Stations
March/April	14	7	7
June	15	8	7
July	16	10	6
August	15	8	7
October	10	5	5
Total	70	38	32

silverside in the collection was identified to species, measured to the nearest mm standard length, and stored for future stomach analyses.

Field data for the inshore and offshore surveys, and the feeding experiments were transcribed onto standard code forms for automatic data processing. The main hardware used for data storage/retrieval was the VIMS Prime 750 computer, a TSO terminal oriented disk system. The major software used for data analyses included SPSS (Statistical Package for the Social Sciences) and other VIMS special purpose programs available through the VIMS computer center program library.

RESULTS

I. Feeding Experiments - Adult Fishes

A) Experiments 1 and 2

Experiments 1 and 2 were designed to assess the food selection of adult Membras and Menidia in sympatry (6 preliminary experiments were used to develop the methods for handling the prey and the fishes). Zooplankton and epibenthic prey were present in the feeding chamber. Five Menidia (94-110 mm) and five Membras (73-87 mm) were present in the tank during experiment 1. Six Menidia (95-108 mm) and six Membras (60-80 mm) were used during experiment 2.

Selection index values derived from the gut contents of Membras were not significantly different from L=0 (random selection) for epibenthic prey (tables 2 and 3). Out of 313 prey items found in 5 Membras stomachs from experiment 1, no gammarid amphipods or isopods were consumed (caprellid amphipods were not available). Out of 2248 prey taken from the 6 Membras stomahcs in experiment 2, only 11 gammarid amphipods (L=.004), 6 isopods (L=.002), and no caprellid amphipods (L=-.0004) were found.

In contrast, selection values of epibenthic prey derived from the stomach contents of Menidia were significantly positive, indicating selection (tables 2 and 3). Out of 691 prey items found in the stomachs of 5 Menidia from experiment 1, 19 were gammarid amphipods

Table 2

Data Summary for Feeding Experiment 1
(see text for symbols definition)

		MENIDIA (N=5)			MEMBRAS (N=5)		
Prey	p_i	r_i	L_i	χ^2	r_i	L_i	χ^2
Acartia tonsa (adults)	.032	.614	.582	1217.7**	.000	-.032	20.9**
A. tonsa (copepodites)	.167	.132	-.035	4.74 NS	.115	-.052	10.0 NS
Oithona sp.	.167	.009	-.158	116.9**	.007	-.160	108.6**
copepod nauplii	.457	.015	-.442	448.9**	.257	-.200	79.0**
barnacle nauplii	<.001	.000	--	--	.079	.079	169.7**
Saphirella sp.	.066	.004	-.062	41.3**	.010	-.056	30.3**
other (zooplankton)	.014	.003	-.011	5.45 NS	.000	-.014	8.46 NS
harpacticoid copepod	.004	.017	.013	12.4 NS	.031	.027	33.5**
gammarid amphipod	.002	.028	.026	44.6**	.000	-.002	.939 NS
isopod	.009	.162	.153	272.5**	.000	-.009	10.22 NS
ostracod	.001	.014	.013	20.5**	.010	.009	11.06 NS

** $p<.01$

Table 3

Data Summary for Feeding Experiment 2
(see text for symbols definition)

		MENIDIA (N=6)			MEMBRAS (N=6)		
Prey	p_i	r_i	L_i	χ^2	r_i	L_i	χ^2
Acartia tonsa (adults)	.012	.085	.073	101.7**	.061	.049	147.5**
A. tonsa (copepodites)	.048	.106	.058	21.5**	.084	.036	36.8**
Oithona sp.	.066	.000	-.066	23.2**	.002	-.064	143.4**
copepod nauplii	.685	.009	-.676	623.5**	.061	-.624	2486.1**
barnacle nauplii	.037	.015	-.022	4.23 NS	.463	.426	2157.9**
Saphirella sp.	.073	.033	-.040	7.32 NS	.009	-.064	126.3**
other (zooplankton)	.095	.012	-.083	26.1**	.121	.026	11.68 NS
harpacticoid copepod	.002	.224	.222	1047.9**	.173	.171	950.6**
gammarid amphipod	$.007^{-1}$	.230	.230	1218.5**	.005	.004	14.45 NS
isopod	$.005^{-1}$	.000	$-.005^{-1}$	.179 NS	.003	.002	6.26 NS
caprellid amphipod	$.004^{-1}$	.088	.088	453.1**	.000	$-.004^{-1}$	.813 NS
ostracod	$.003^{-1}$	.052	.051	252.0**	.017	.017	88.0**

** $p<.01$

(L=.026, p<.01) and 112 were isopods (L=.153, p<.01). During experiment 2, the 6 Menidia collectively consumed 330 prey, 76 of which were gammarid amphipods (L=.230, p<.01), and 29 of which were caprellid amphipods (L=.088, p<.01). No isopods were taken. The selection index for isopods was not significantly different from 0 (random selection).

Selection values for pelagic prey were somewhat inconsistent between experiments 1 and 2. In experiment 1, the pooled stomachs of Menidia contained 424 adult Acartia tonsa copepods; a highly significant positive index resulted (L=.582, p<.01). Membras in the same experiment consumed no adult A. tonsa, and a significantly negative index value (indicating avoidance or inaccessability) resulted (L=-.032, p<.01). Analysis of experiment 2 data yielded positive selection values for A. tonsa adults for both Menidia (L=.073, p<.01) and Membras (L=.049, p<.01). Random selection for A. tonsa copepodites occurred in both species during experiment 1; positive selection by both species was indicated for this prey in experiment 2 (L=.058, p<.01 for Menidia and L=.036, p<.01 for Membras). The cyclopoid copepod, Oithona sp., was consistently avoided by Menidia and Membras (p<.01).

Copepod nauplii were strongly avoided or inaccessible to Menidia and Membras (p<.01) although they were the numerically dominant prey in both experiments (p_i=.457 and .685 respectively). Barnacle nauplii were relatively rare in the environment during experiments 1 (p_i <.001) and 2 (p_i=.037). Although barnacle nauplii were similar in

size to copepod nauplii, a relatively high positive selection was derived for barnacle nauplii from the gut contents of Membras in both experiments (L=.079, p<.01 and L=.426, p<.01 respectively). In contrast, Menidia in experiment 1 ate no barnacle nauplii and randomly selected them in experiment 2.

Selection of harpacticoids by Menidia was not significantly different from L=0 in experiment 1, but a significantly positive selection value for them was seen in experiment 2 (p<.01). Membras selectively incorporated harpacticoids in its diet in both experiments (L=.027, p<.01 and L=.171, p<.01 respectively).

B) Experiments 3 and 4 - Membras allopatry

Food selection of adult Membras in allopatry was assessed in experiments 3 and 4. Zooplankton and epibenthic prey was present in the feeding chamber and density of prey types were reasonably consistent with former experiments. Natural fluctuations in species composition of the prey collected from the wild were present. Therefore the proportions of prey species were not precisely equal to previous experiments. Six individuals were used per test (size range 82-90 mm for experiment 3 and 84-95 mm for experiment 4).

The pooled stomach contents from both experiments contained no gammarid amphipods, isopods, or caprellids amphipods, even though these prey were present in the feeding chamber at densities which were equivalent to former experiments. All selection indices for these epibenthic prey were not significantly different from L=0, except for

significant avoidance of isopods by Membras in experiment 4 ($L=-.008$, $p<.05$, table 4).

A. tonsa adults were selected in both experiments 3 ($L=.195$, $p<.01$) and 10 ($L=.023$, $p<.01$). Random selection occurred with respect to A. tonsa copepodites in experiment 3 and significant avoidance was found in experiment 4 ($L=-.028$, $p<.01$).

Selection values of Oithona sp. in experiment 1 and 2 indicated that in the presence of Menidia, Membras were avoiding or could not capture Oithona sp. However, when Membras were alone in the chamber selection was found for Oithona sp. (experiment 3, $L=.109$, $p<.01$) even though the environmental proportion of Oithona sp. in experiment 2 ($p_i=.066$) was similar to the p_i for experiment 3 ($p_i=.075$). Oithona sp. was also significantly selected for by Membras in experiment 4 ($L=.365$, $p<.01$).

Copepod nauplii were again highly avoided or inaccessible in experiments 3 and 4 although copepod nauplii were by far the most numerous prey species. Barnacle nauplii were rare in the environment, but significant selection for them was found in both experiments ($L=.072$, $p<.01$ and $L=.053$, $p<.01$ respectively).

C) Experiment 5 and 6 - Menidia allopatry

Two experiments were planned for the Menidia allopatry experiments. Test fish in experiment 5 ate very little; the data were inadequate for meaningful analysis and are excluded from this report. I was unable to repeat the experiment, thus the Menidia allopatry

Table 4

Data Summary for Feeding Experiments 3 and 4, *Membras* in allopatry
(see text for symbols definition)

	EXPERIMENT 3 (N=6)				EXPERIMENT 4 (N=6)			
Prey	p_i	r_i	L_i	χ^2	p_i	r_i	L_i	χ^2
Acartia tonsa (adults)	.017	.212	.195	869.2**	.020	.043	.023	15.56**
A. tonsa (copepodites)	.014	.026	.012	14.4 NS	.049	.021	-.028	23.78**
Oithona sp.	.075	.184	.109	196.1**	.434	.799	.365	574.9**
Paracalanus sp.	$.008^{-1}$	.002	.002	2.68 NS	.029	.012	-.017	16.41*
copepod nauplii	.817	.018	-.799	4188.8**	.610	.019	-.589	1836.8**
barnacle nauplii	.009	.081	.072	283.5**	.023	.076	.053	50.5**
Saphirella sp.	.020	.061	.041	83.4**	.017	.023	.006	1.48 NS
other (zooplankton)	.004	.012	.008	15.26*	.004	.000	-.004	9.57 NS
harpacticoid copepod	$.001^{-1}$	.007	.007	37.4**	.001	.003	.002	3.11 NS
gammarid amphipod	$.001^{-1}$	.000	$-.001^{-1}$	.131 NS	.001	.000	-.001	3.10 NS
isopod	$.002^{-1}$	.000	$-.002^{-1}$	.048 NS	$.001^{-1}$	.000	$-.001^{-1}$	.335 NS
caprellid amphipod	$.002^{-1}$	.000	$-.002^{-1}$	.546 NS	.008	.000	-.008	19.5*
ostracod	$.002^{-2}$	.021	.021	112.4**	$.005^{-1}$	.001	$.006^{-1}$	.433 NS
other (epibenthic)	$.001^{-1}$	.000	$-.001^{-1}$	.236 NS	.001	.003	.002	.998 NS

* $p<.05$ ** $p<.01$

testing reported here is limited to experiment 6 in which six fishes were used (size range 91-112 mm).

Out of 2539 prey items found in the stomachs of six Menidia, 18 were gammarid amphipods (L=.005), and 30 were caprellid amphipods (L=.007). No isopods were ingested. Index values for epibenthic prey were not significantly different from L=0 (table 5). The Menidia were feeding mainly on pelagic zooplankton. Although this suggests that in the absence of competition for zooplankton by Membras, Menidia were able to exploit the pelagic community, such a conclusion cannot be made on the basis of one experiment.

Paracalanus sp. and barnacle nauplii in experiment 6 were the preferred zooplankton prey of Menidia (L=.024, $p<.01$ and L=.108, $p<.01$ respectively). Oithona sp. was avoided (L=-.204, $p<.01$) as were copepod nauplii (L=-.344, $p<.01$). In decreasing order of importance, Menidia selected harpacticoids (L=.077, $p<.01$), ostracods (L=.054, $p.<.01$), and A. tonsa adults (L=.034, $p<.01$). A. tonsa copepodites were randomly selected.

II. Ontological Changes in Diet

Intraspecific food selection between various sizes of individual fishes was tested in experiments 7 and 8. Ten Membras were used in experiment 7 (size range 32-96 mm FL), and 13 Menidia in experiment 8 (size range 51-85 mm FL). Experiment 8 was undertaken later in the fall of 1981 when Menidia smaller than 50 mm were unavailable. Since previous experiments showed that Membras did not prey on epibenthic organisms, only zooplankton were used in experiment 7; epibenthic and

Table 5

Data Summary for Feeding Experiment 6, *Menidia* in Allopatry
(see text for symbols definition)

	MENIDIA (N=5)			
Prey	p_i	r_i	L_i	χ^2
Acartia tonsa (adults)	.002	.036	.034	19.36*
A. tonsa (copepodites)	.016	.031	.015	3.75 NS
Oithona sp.	.507	.303	-.204	72.8**
Paracalanus sp.	.053	.293	.240	130.0**
copepod nauplii	.364	.020	-.344	701.2**
barnacle nauplii	.021	.129	.108	55.4**
Saphirella sp.	.013	.016	.003	.263 NS
other (zooplankton)	.007	.013	.006	1.61 NS
harpacticoid copepod	.008	.085	.077	42.1**
gammarid amphipod	.002	.007	.005	2.28 NS
isopod	$.007^{-2}$	.000	$-.007^{-2}$	.170 NS
caprellid amphipod	.005	.012	.007	1.95 NS
ostracod	.002	.056	.054	32.1**
other (epibenthic)	$.007^{-2}$	.000	$-.007^{-2}$	.170 NS

* $p<.05$ ** $p<.01$

zooplanktonic prey were present in experiment 8. Selection values from experiments 7 and 8 for the most important prey species were regressed with fork length (figures 5-11).

The slope (β) of each regression line was tested for significance (H_o: $\beta=0$, H_i: $\beta \neq 0$) with the SPSS regression procedure ($F = \frac{SS_{reg}}{SS_{res/N-2}}$), and the coefficient of determination (R^2) was calculated. Since L is distributed approximately normally (Strauss 1979), the distributional conditions for the regression analysis were satisfied.

A) Experiment 7 - Membras

The regression of L_i for Acartia tonsa adults vs fish length was significantly positive (β = .796); R^2 was 0.633 (figure 5). The slopes of the regressions for all the other prey species: A. tonsa copepodites, Oithona sp., Paracalanus sp., copepod and barnacle nauplii, Sapherella sp., and harpacticoids were not significantly different from zero. The data clustered around L=0 for A. tonsa copepodites (figure 5), barnacle nauplii (figure 6), and Paracalanus sp. (figure 7). Copepod nauplii were avoided or inaccesible (figure 6), and Oithona sp. (figure 7) were selected throughout the range of fish lengths, but to a linear degree as fish size increased.

B) Experiment 8 - Menidia

Regressions of L_i vs fork length with slopes significantly greater or less than zero were generated in the analysis of Acartia tonsa adults and copepodites, and caprellid amphipod selectivity. The regression of L_i vs fish length for Acartia tonsa adults had a

Figure 5. Regression of the linear index (L_i) vs fish length for Membras martinica in the selection of Acartia tonsa adults and copepodites, experiment 7.

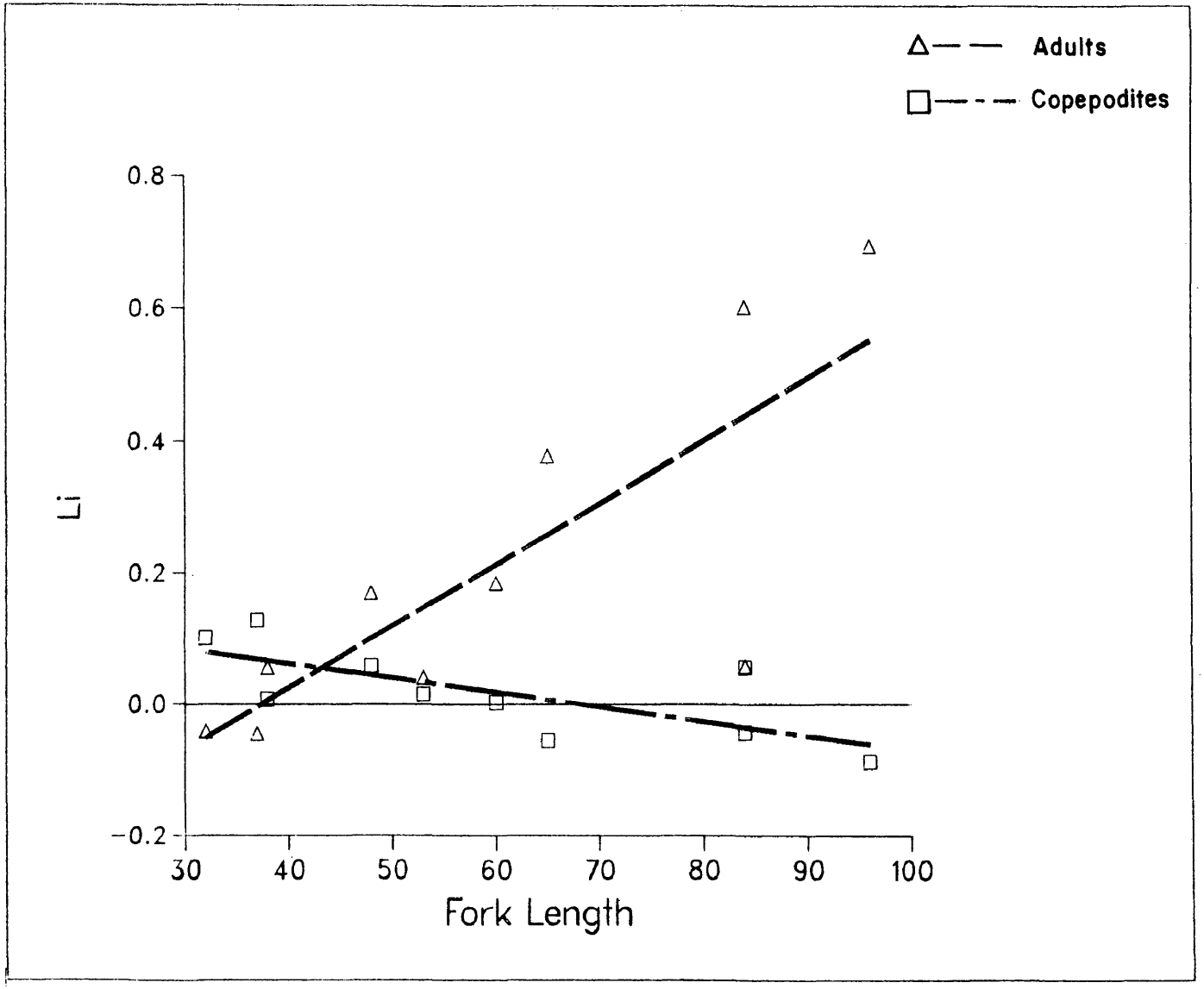

Adults
Copepodites
0.8
0.6
0.4
0.2
0.0
-0.2
Li
30
40
50
60
70
80
90
100
Fork Length

Figure 6. Regression of the linear index (L_i) vs fish length for Membras martinica in the selection of copepod and barnacle nauplii, experiment 7.

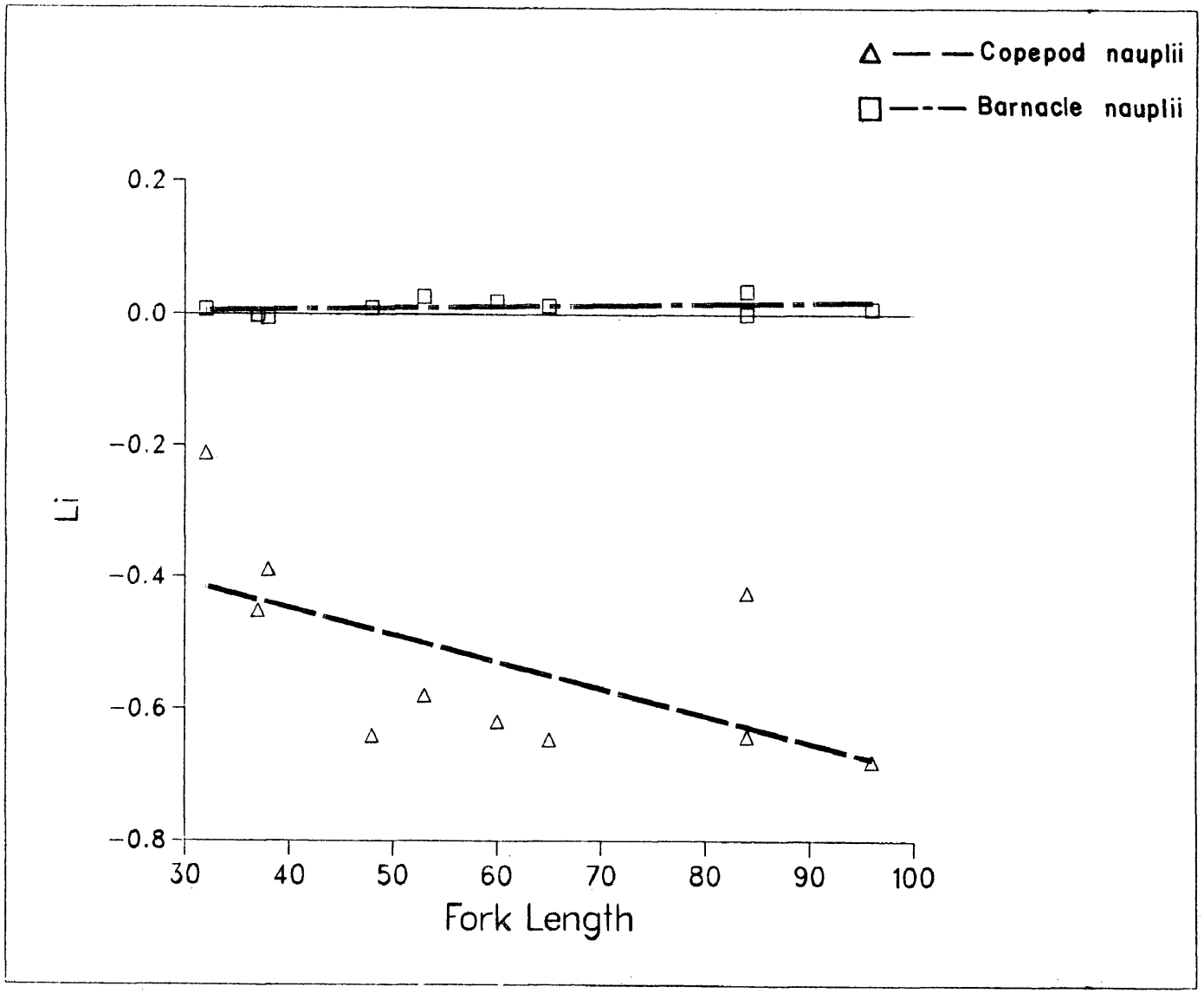

Copepod nauplii
Barnacle nauplii
0.2
0.0
-0.2
-0.4
-0.6
-0.8
Li
30
40
50
60
70
80
90
100
Fork Length

Figure 7. Regression of the linear index (L_i) vs fish length for Membras martinica in the selection of Oithona sp. and Paracalanus sp., experiment 7.

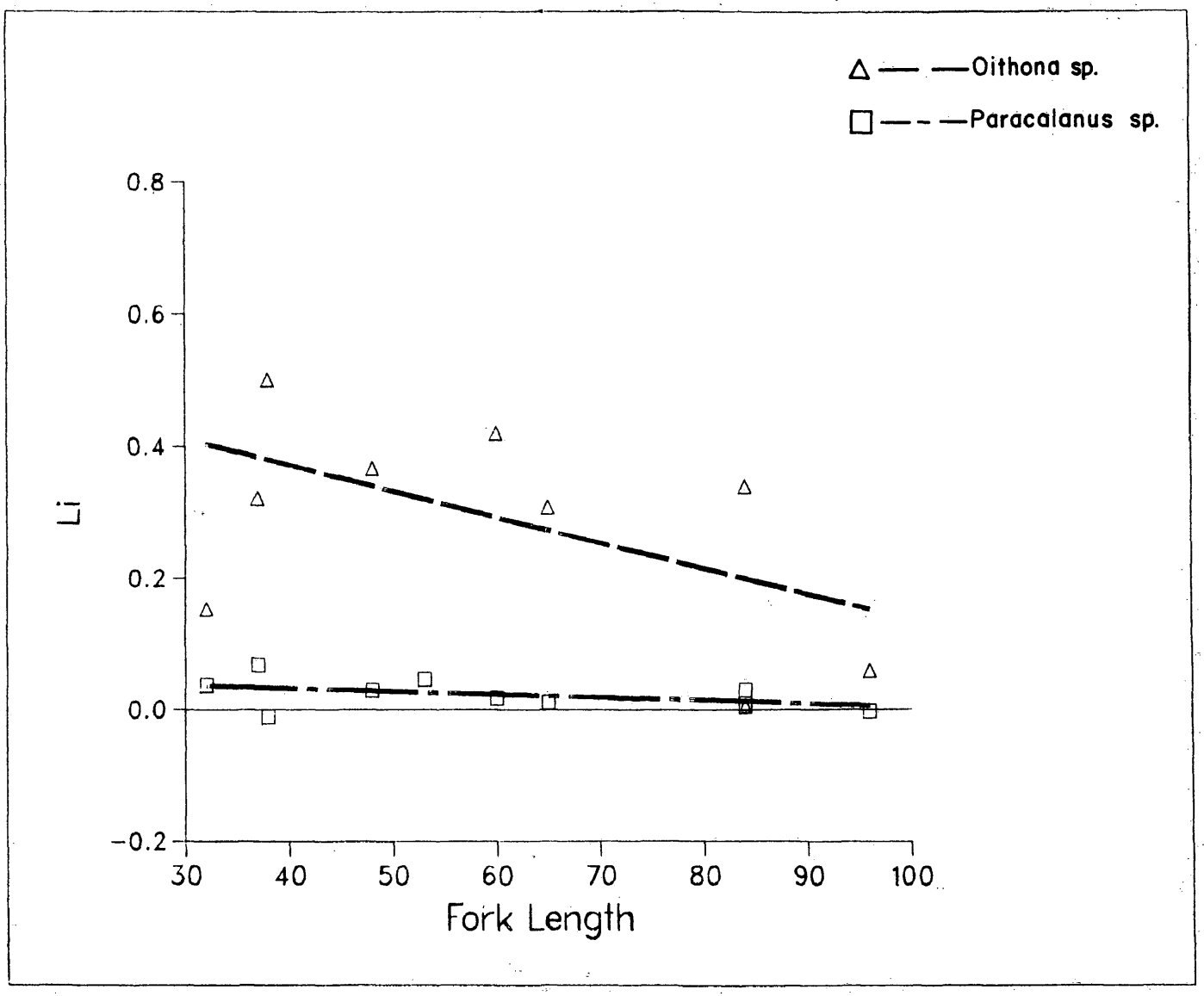

Oithona sp.
Paracalanus sp.
0.8
0.6
0.4
0.2
0.0
-0.2
Li
30
40
50
60
70
80
90
100
Fork Length

Figure 8. Regression of the linear index (L_i) vs fish length for Menidia menidia in the selection of Acartia tonsa adults and copepodites, experiment 8.

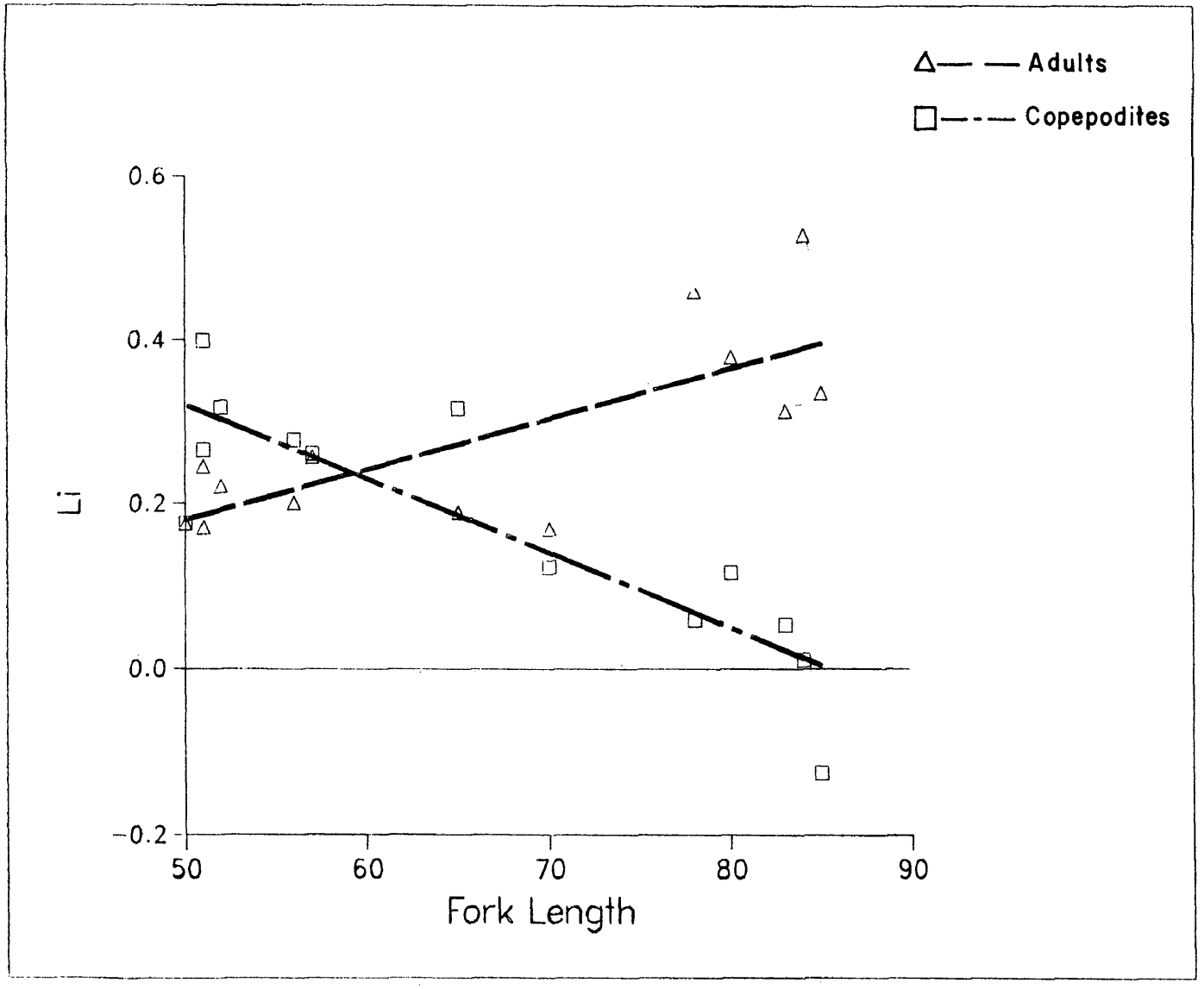

Adults
Copepodites
0.6
0.4
0.2
0.0
-0.2
50
60
70
80
90
Fork Length

Figure 9. Regression of the linear index (L_i) vs fish length for Menidia menidia in the selection of caprellid amphipods, experiment 8.

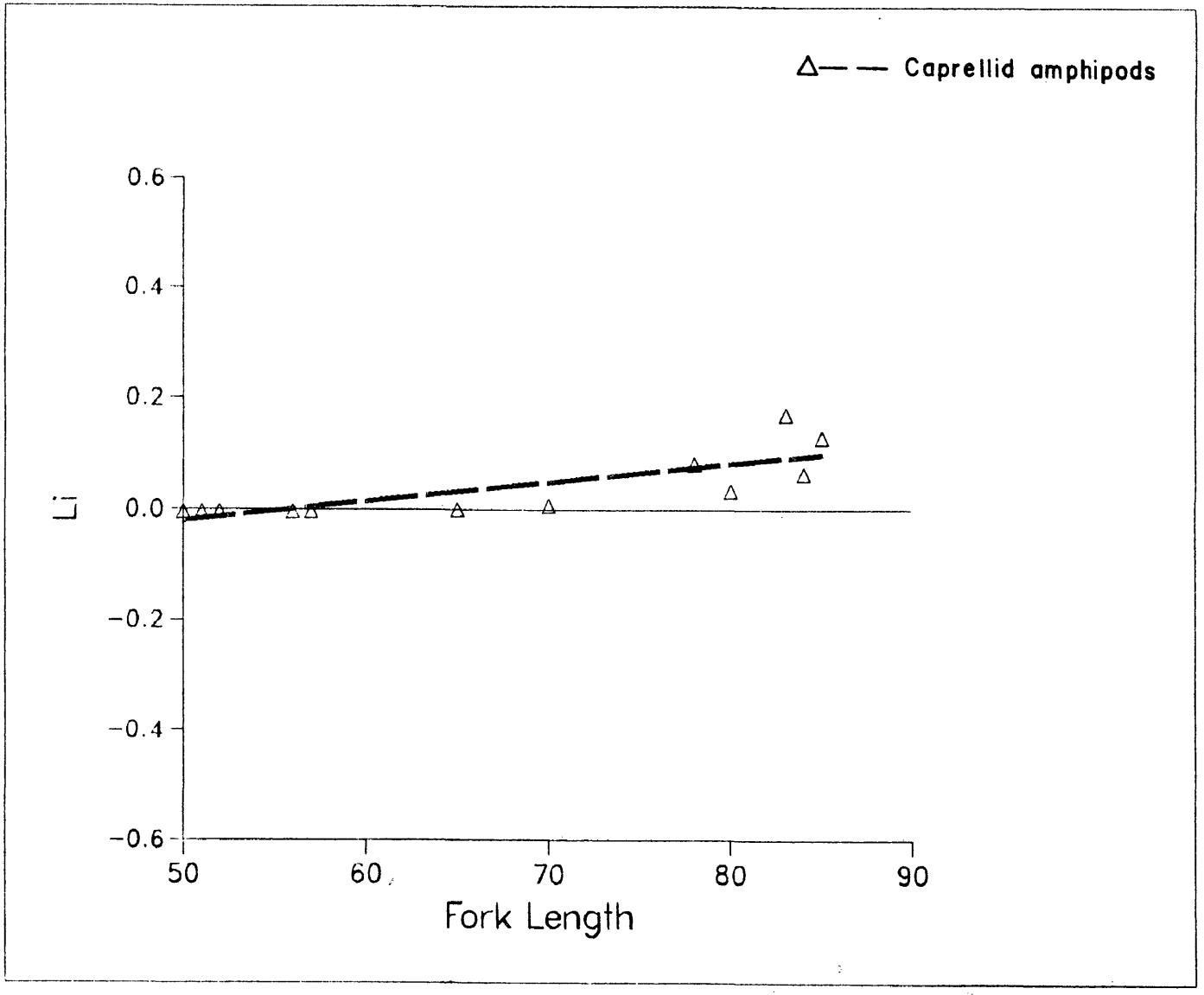

Caprellid amphipods
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
50
60
70
80
90
Fork Length

Figure 10. Regression of the linear index (L_i) vs fish length for *Menidia menidia* in the selection of copepod and barnacle nauplii, experiment 8.

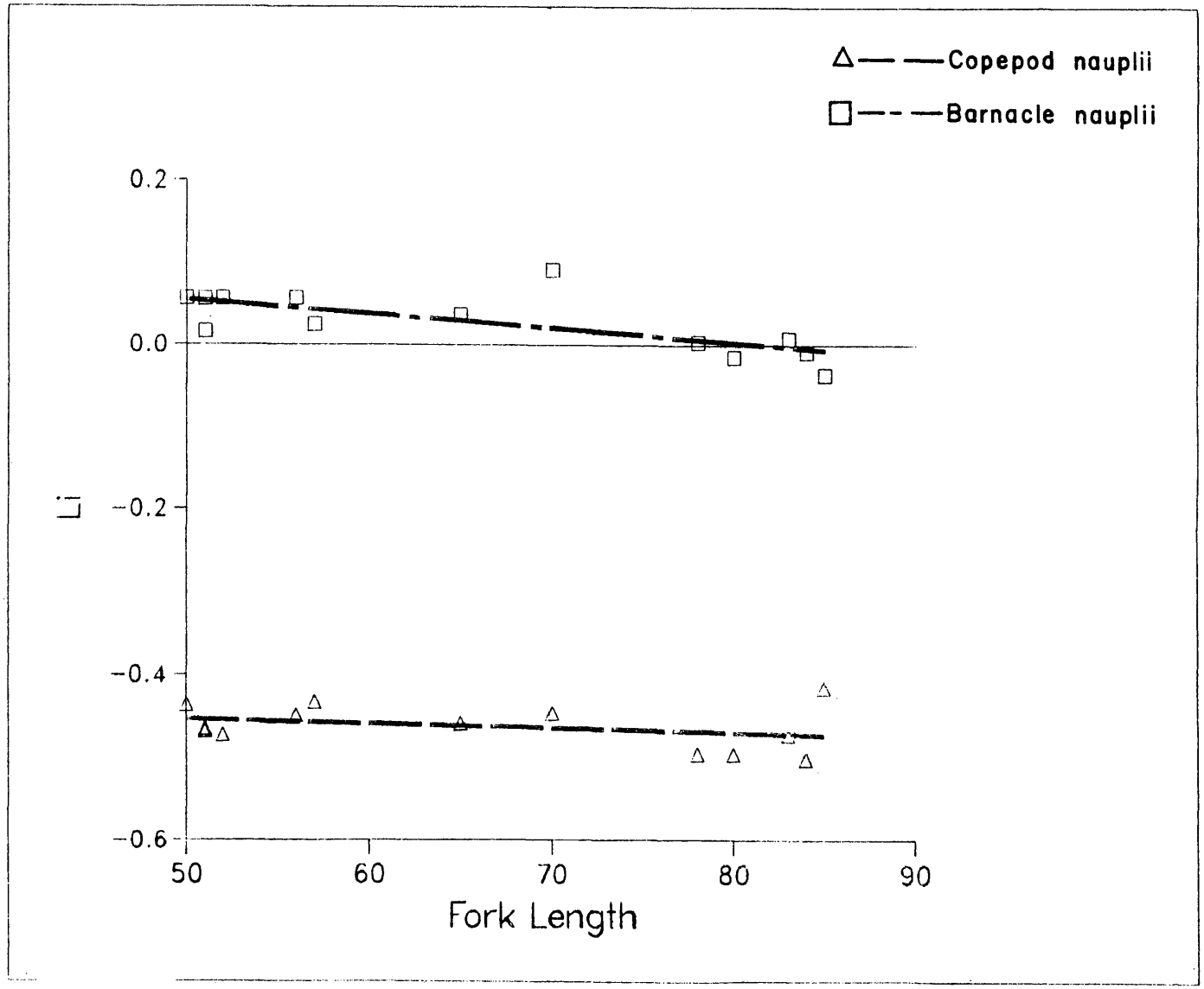
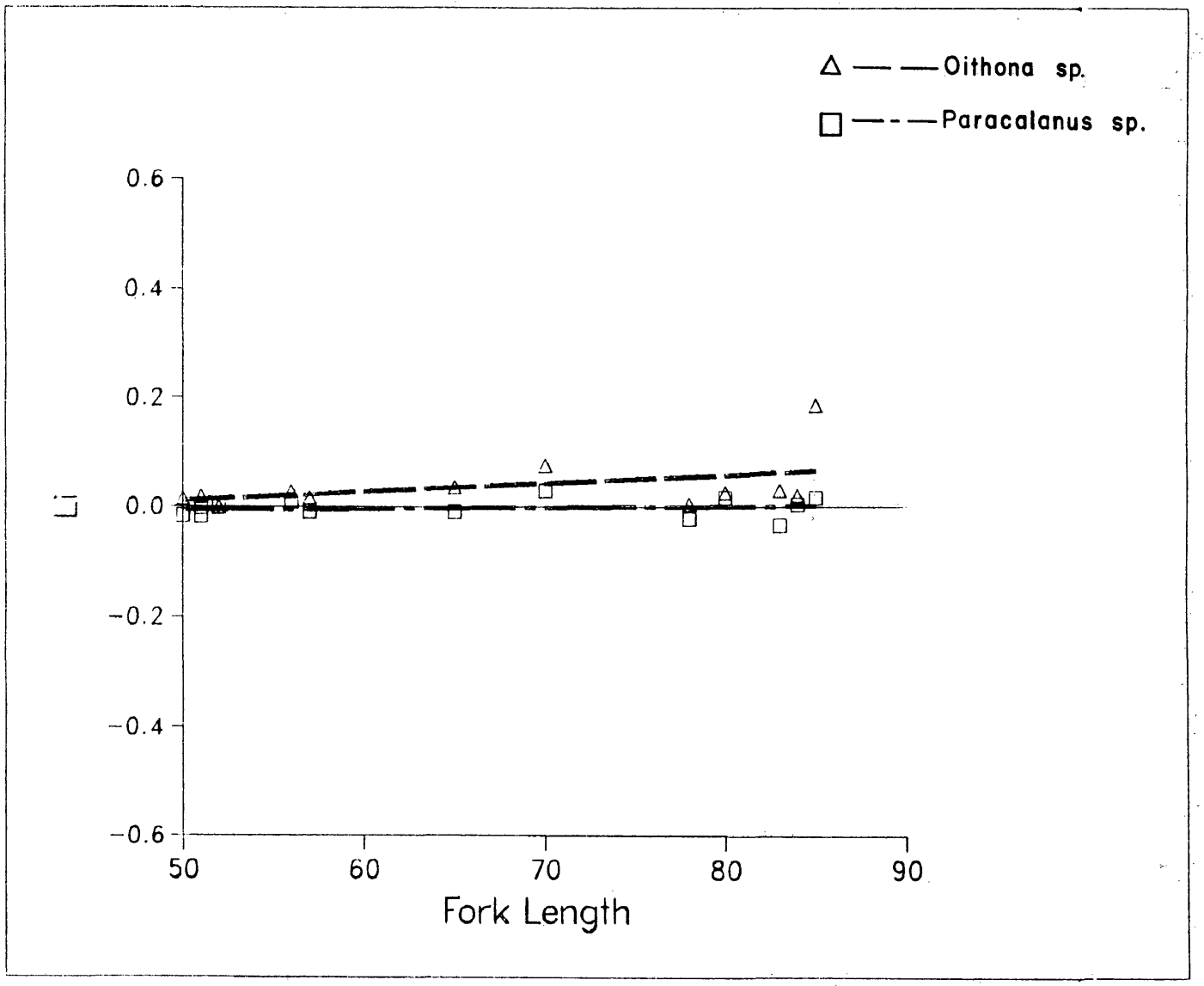

Copepod nauplii
Barnacle nauplii
0.2
0.0
−0.2
−0.4
−0.6
50
60
70
80
90
Fork Length

Figure 11. Regression of the linear index (L_i) vs fish length for *Menidia menidia* in the selection of *Oithona* sp. and *Paracalanus* sp., experiment 8.


Oithona sp.
Paracalanus sp.
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
50
60
70
80
90
Fork Length

positive slope (β =.754, R^2=0.568), indicating that larger Menidia preyed more heavily on adults (figure 8). Conversely, the regression for A. tonsa copepodites (figure 8) had a negative slope (β =-.858, R^2=0.737). Caprellid amphipods (figure 9) were ingested by fishes greater than 65 mm. The regression had a positive slope (β =.814) and a coefficient of determination (R^2) of 0.663. The slopes for the regression of Oithona sp., copepod and barnacle nauplii, and Paracalanus sp. were not significantly greater or less than zero. The selection indices were near or at zero for barnacle nauplii (figure 10), Oithona sp., and Paracalanus (figure 11). Copepod nauplii were consistently avoided by all sizes of Menidia (figure 10).

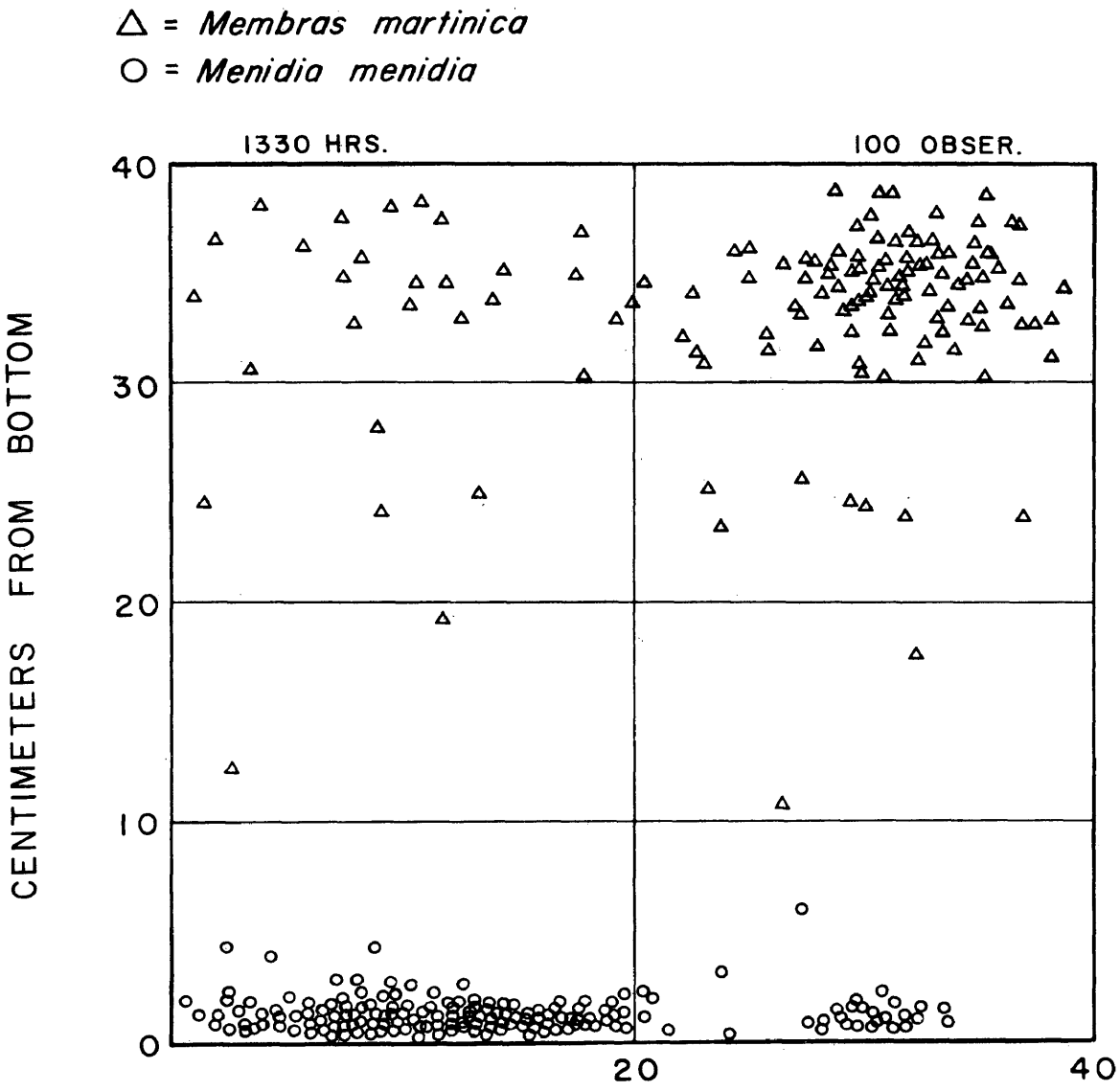
III. Vertical Distribution

A) Laboratory Experiments

Five laboratory experiments examined vertical distribution of adult Membras and adult Menidia. The first experiment simulated daytime conditions with six Menidia and six Membras in sympatry. Ample quantities of planktonic and epibenthic prey were provided. Feeding behavior was observed in all fishes.

In daylight Membras oriented at or near the surface in loose aggregates (figure 12). The majority of the fishes remained in the top ten centimeters of the grid. Fewer fish were observed in the 20 to 30 centimeter depth interval, and even fewer in the 10 to 20 increment. No Membras occurred in the first 10 centimeters from the bottom. Menidia on the other hand never occurred above ten centimeters from the bottom of the tank (figure 12). Individual fish

Figure 12. Vertical distribution of Membras martinica and Menidia menidia in sympatry during daylight experiment. A total of 100 observation periods are plotted for each species. Six Menidia and six Membras were present in the tank.


△ = Membras martinica
○ = Menidia menidia
1330 HRS.
100 OBSER.
CENTIMETERS FROM BOTTOM
40
30
20
10
0
20
40

remained in close association with others of its species, and usually moved about in groups of two or three fishes.

Daytime single species experiments in the tank resulted in vertical distributions identical to the sympatry tests cited above (figures 13A and 14A). Hence, it is unlikely that the observed bimodal vertical distribution was a function of direct competitive interaction between Menidia and Membras.

Vertical distributions in the nightime revealed dispersal of both Menidia and Membras in darkness (the same test fishes that were used in day and night experiments). Membras were evenly distributed between the 10 to 40 centimeter intervals off the bottom and only a few fish were observed in the 0 to 10 centimeter section (figure 13B). At night Menidia were no longer in tight groups and tended to move off the bottom slightly (figure 14B) but none entered the 30-40 cm interval.

B) Vertical Distribution - Special Field Sampling

Membras adults and juveniles were the only atherinid species caught in subsurface collections at night in the open waters of the lower Chesapeake Bay. Therefore, the results of the laboratory observations could be easily compared with the vertical distribution of fishes in the field. During the October 1981 lower bay cruise, three discrete depths were fished using the rectangular net (table 6). Membras were caught only in the 0-.5 meter interval. Results of the rectangular trawls suggest that the downward distribution of Membras at night does not exceed 0.5 meters. Stepped oblique bongo net tows

Figure 13. Vertical distribution of Membras martinica in allopatry, A) daylight B) darkness. Fifty observation periods are plotted for each period. Eight fish were in the tank.

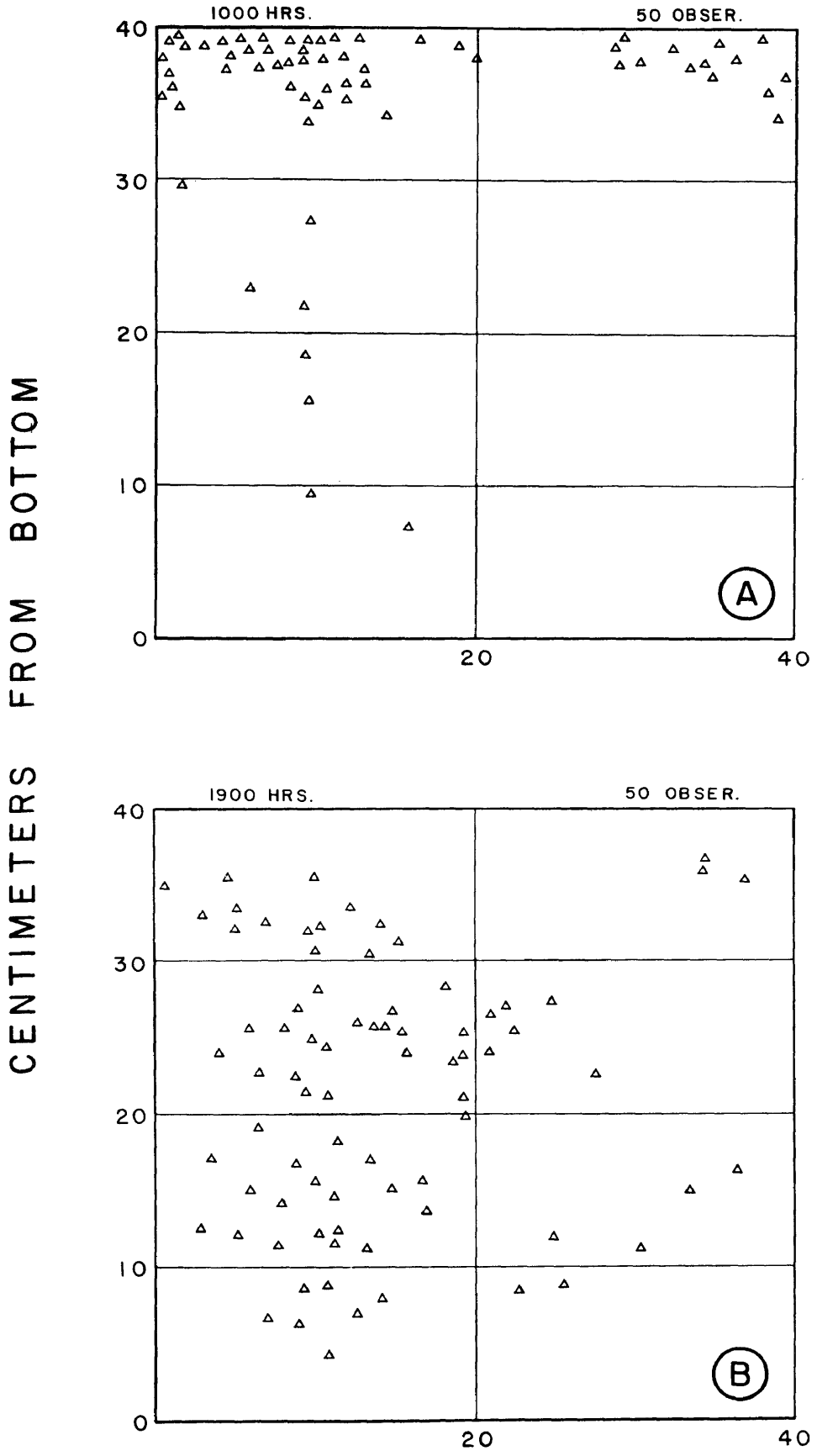

1000 HRS.
50 OBSER.
40
30
20
10
0
20
40
A
1900 HRS.
50 OBSER.
40
30
20
10
0
20
40
B
CENTIMETERS FROM BOTTOM

Figure 14. Vertical distribution of Menidia menidia in allopatry, A) daylight B) darkness. Forty observation periods are plotted for daylight; 30 for darkness. Nine fish were in the tank.

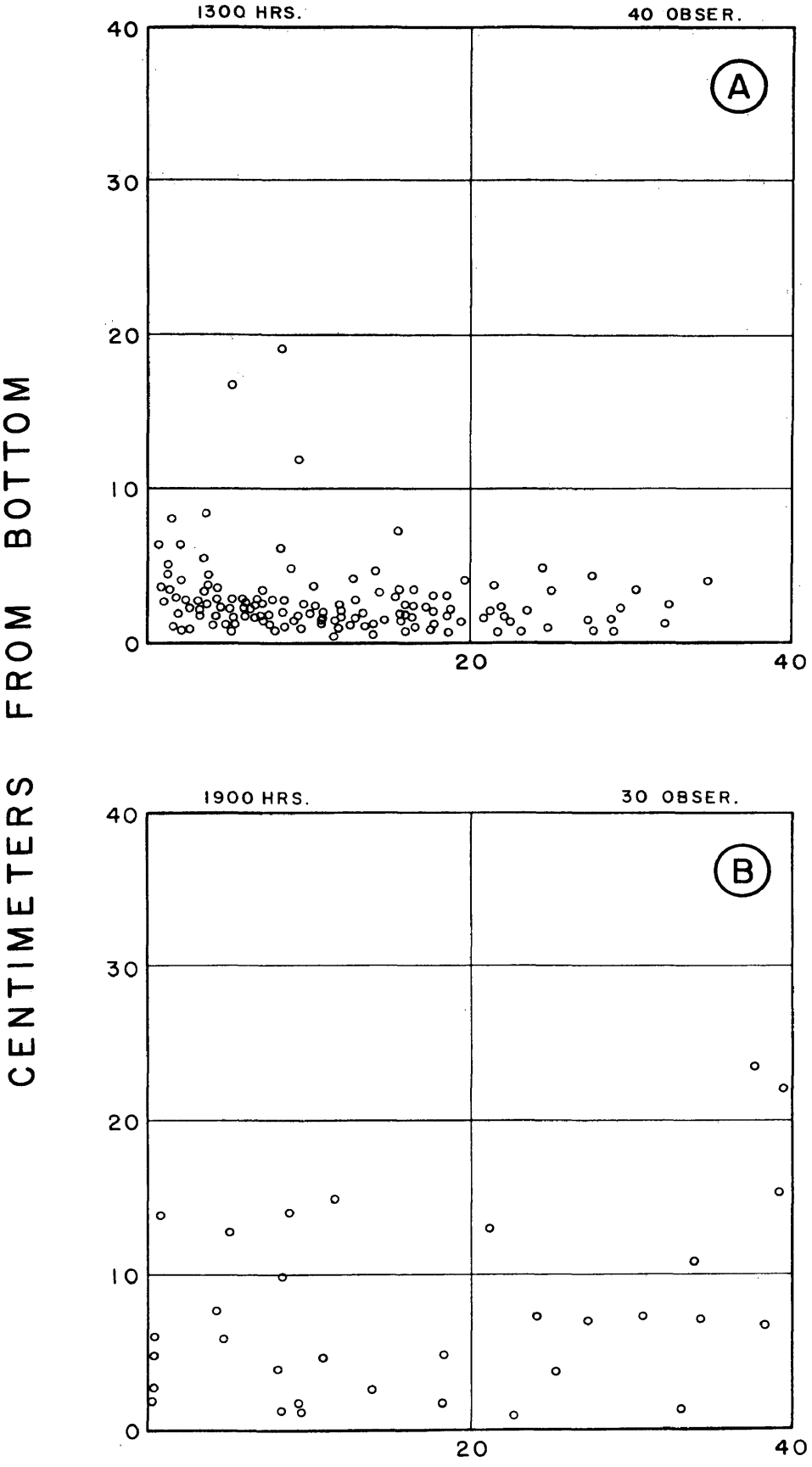

1300 HRS.
40 OBSER.
A
40
30
20
10
0
20
40
CENTIMETERS FROM BOTTOM
1900 HRS.
30 OBSER.
B
40
30
20
10
0
20
40

Table 6

Numbers of *Membras* captured at night in 10 minute rectangular frame tows during the lower bay zooplankton survey, October 1981.

Station	Time (EST)	Fishing Depth (M)	# of Membras/10 min
323	2130	0-.5	66
430	1955	1.0-1.5	0
488	1755	1.5-2.0	0

taken at each station (in two meter depth intervals) caught few Membras. Those that were captured were probably caught as the net passed through the surface layer.

On calm nights in midsummer, about 1 Membras every square meter were seen slowly swimming just a few centimeters below surface at most stations. In view of these observations, the laboratory results of a downward movement in the water column at night by Membras may have been an artifact of restriction of the fishes in a confined tank. Based on the results of the present study it is probable that Membras disperse horizontally at night but remain in the upper 1/2 meter.

IV. Offshore Distribution

Membras martinica occurred in large numbers in the 1981 lower bay zooplankton neuston collections. No Menidia menidia were found offshore. Significant differences in length frequency distribution were found between day and night samples (figure 15), with the exception of June and October collections. No atherinids were taken in the April/March survey.

Only 5-19 mm SL (standard length) individuals were taken in June. Day and night length frequencies were not significantly different (table 7). Of all months surveyed, the average density per station was lowest in June. Day and night densities were 2.4 and 1.7 fish/10 m^2 respectively.

In July the standard length of fish in day collections was strikingly smaller than in night collections (figure 15 and table 7).

Figure 15. Length frequency distributions of Membras martinica in open bay waters by month for 1981.

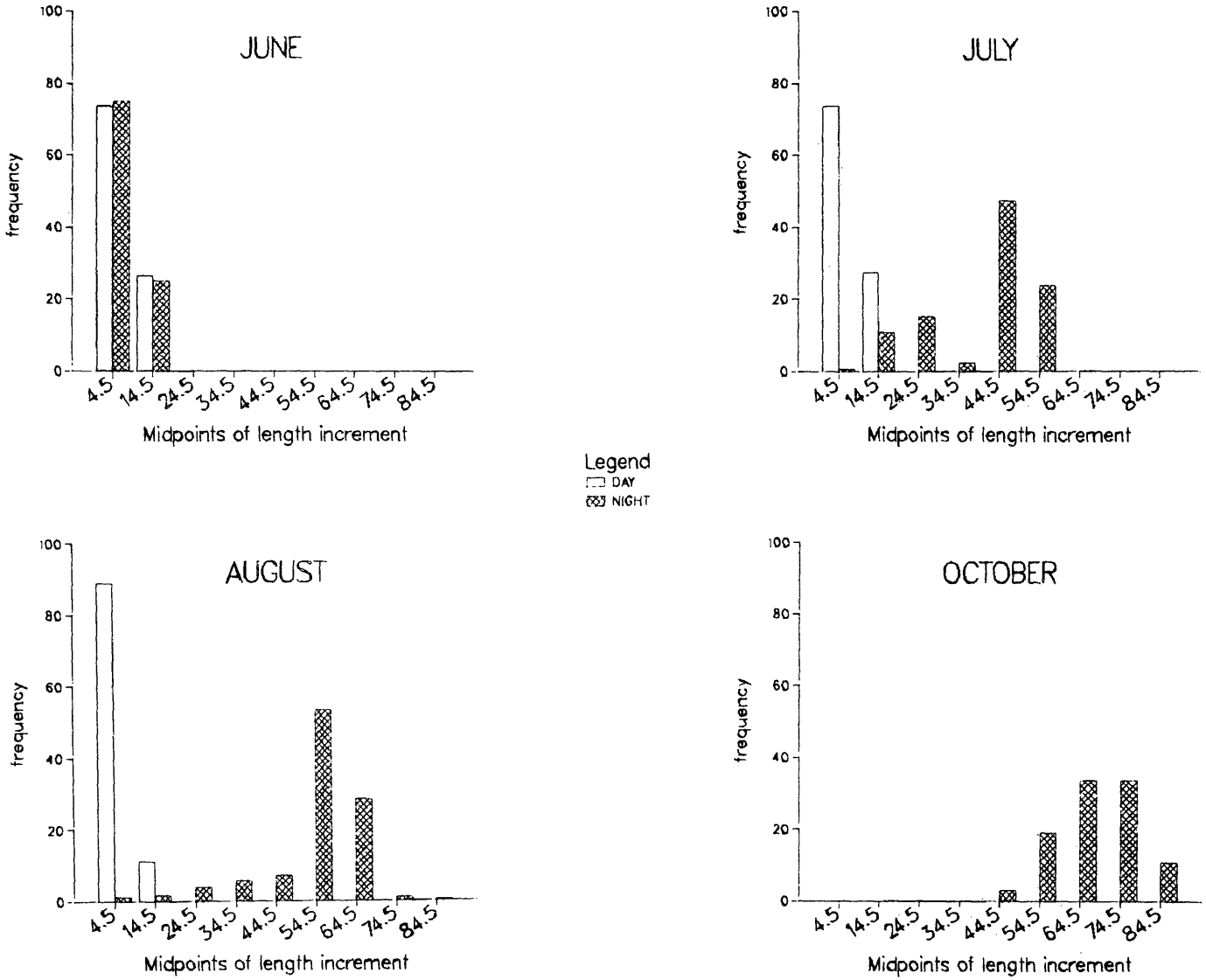

JUNE
JULY
AUGUST
OCTOBER
frequency
Midpoints of length increment
4.5
14.5
24.5
34.5
44.5
54.5
64.5
74.5
84.5
0
20
40
60
80
100
Legend
DAY
NIGHT

Table 7

Length Frequencies of surface-caught Membras martinica from the 1981 Offshore Survey

			Midpoint of Standard Length interval (mm)									
			4.5	14.5	24.5	34.5	44.5	54.5	64.5	74.5	84.5	tot.
June	Day	N	28	10	-	-	-	-	-	-	-	38
		%	73.7	26.3	-	-	-	-	-	-	-	
	Night	N	15	5	-		-	-	-	-	-	20
		%	75.0	25.0	-		-	-	-	-		
July	Day	N	40	15	-		-	-	-	-		55
		%	73.7	27.3	-	-	-	-	-	-		
	Night	N	3	54	76	12	237	119	1	-		502
		%	0.6	10.8	15.1	2.4	47.2	23.7	0.2	-		
August	Day	N	128	16	-	-	-	-	-	-	-	144
		%	88.9	11.1	-	-	-	-	-	-	-	
	Night	N	9	13	27	43	53	398	197	7	2	749
		%	1.2	1.7	3.8	5.7	7.1	53.1	28.3	0.9	0.3	
October	Day	N	-	-	-	-	-	-	-	-	-	0
		%	-	-	-	-	-	-	-	-	-	
	Night	N	-	-	-	-	4	25	44	44	14	131
		%	-	-	-	-	3.1	19.1	33.6	33.6	10.7	

Forty-seven percent of the fishes taken at night in July were in the 40-49 mm size interval. The mean density (fish/10 m^2) was 3.8 during the day and 30.6 at night.

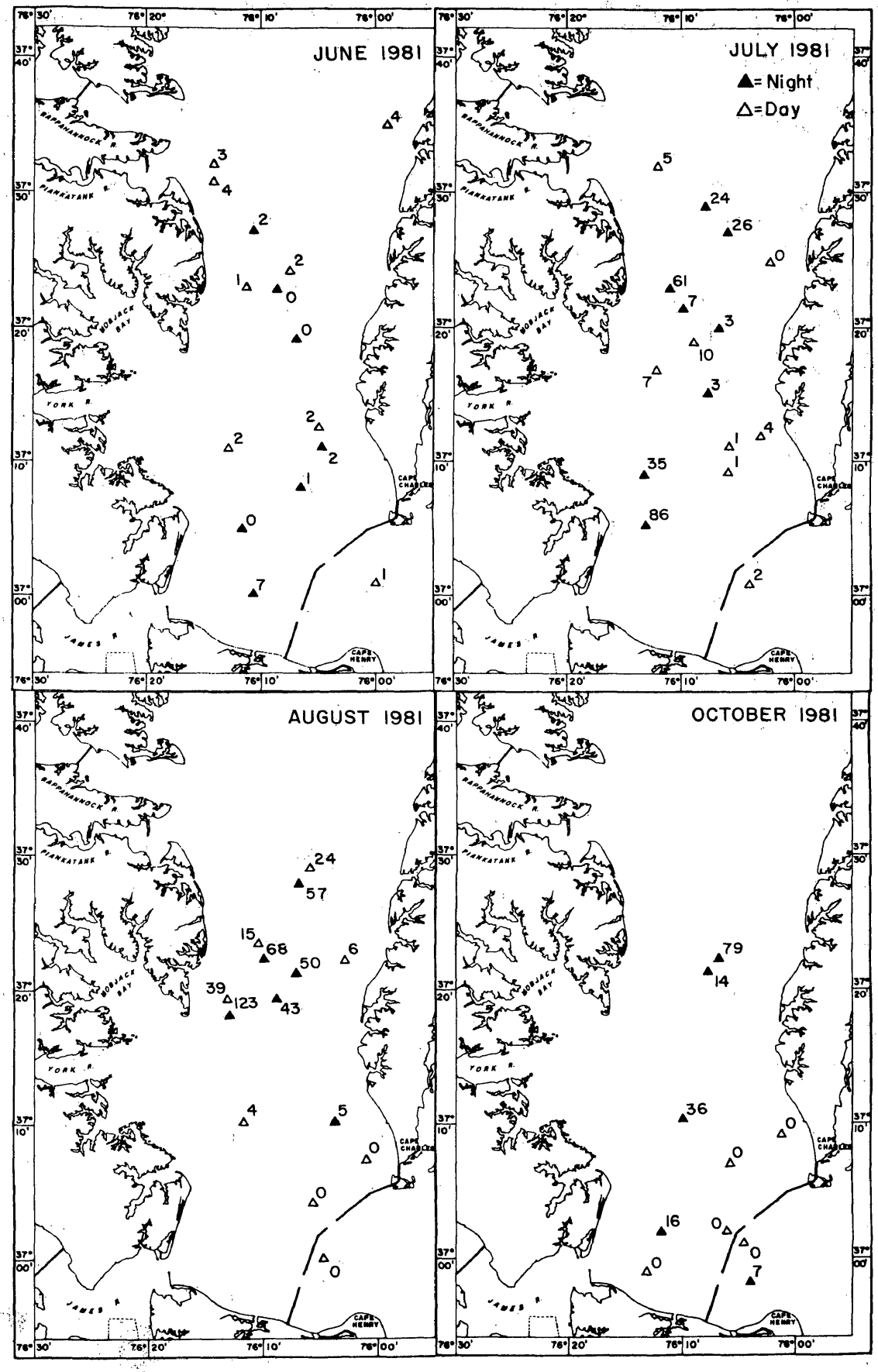
The density of Membras peaked in August. Average daytime density (#/10 m^2) was 11.0 ,in contrast to 57.7 at night. Samples collected in daylight were dominated by 5-19 mm juveniles. At night the size range was 5-90 mm but fifty-three percent of the fish were in the 50-59 mm increment (table 7).

The average nightime density dropped in October to 30.4 individuals/10 m^2. No atherinids were caught in daylight collections. Sixty-seven percent of the captured fish measured between 60-79 mm, and none were smaller than 40 mm (table 7).

During darkness Membras were observed to be widely spaced on the surface in random nonpolarized aggregates. On a calm night hundreds were seen slowly swimming near the surface. In daylight they were no longer randomly distributed. Areas that were teaming with Membras at night were completely devoid of them by daylight. Therefore, the day/night differences in length frequencies and abundances reflected in the above data can not be attributed solely to gear avoidance.

In figure 16 the density of adult and juvenile Membras has been plotted on the grid of station locations in the lower Chesapeake by month. Only juvenile Membras were captured in June. The juveniles were evenly distributed throughout the range of stations; the adults were most likely spawning inshore (Martin and Drewry, 1978). In July

Figure 16. The distribution of Membras martinica adults and juveniles in the lower Chesapeake Bay. Stations located in the 1981 Lower Bay Zooplankton Monitoring Survey are plotted. Adjacent numbers indicate density of adult and juvenile Membras/10 m^2.


JUNE 1981
JULY 1981
▲= Night
△=Day
AUGUST 1981
OCTOBER 1981
RAPPAHANNOCK R.
PIANKATANK R.
MOBJACK BAY
YORK R.
JAMES R.
CAPE HENRY
CAPE CHARLES
76° 30'
76° 20'
76° 10'
76° 00'
37° 40'
37° 30'
37° 20'
37° 10'
37° 00'

and August both adult and juvenile fishes occurred in the collections. Their distribution appears patchy in all months with no apparent near shore to offshore gradient in abundance. Densities at night stations ranged from 3 to 86 fishes/10 m^2 in July and from 5 to 123 fishes/10 m^2 in August. Night collections in October ranged from 7 fishes/10 m^2 outside the bridge tunnel to 79 fishes/10 m^2 at the northernmost station. Since the sampling effort was concentrated north of the bridge tunnel, little can be stated on the occurrence of Membras outside the bay.

V. Inshore Distribution

Menidia menidia were the dominant atherinid species in the 1980 and 1981 beach seine surveys. The mean catch per unit effort (CPUE) for Menidia was 21.7 and 30.1 fishes per haul in 1980 and 1981, respectively. Membras were much less abundant with an average CPUE of 1.1 in 1980 and 0.6 in 1981. Judging from the scarcity of Membras in the upriver area and to their greater abundance in the open bay, near shore environments are clearly not their preferred habitats. Obviously, Menidia utilize shallow inshore zones to a great extent (table 9).

Peak abundances of Menidia were in salinities ranging from 4.0 to <24.0 PPT in 1980 and 1981 (table 8). Membras did occur near shore with some regularity in salinities ranging from 0-3.9 PPT; the CPUE (2.1) in 1980 was nearly three times higher than the combined CPUE of the remaining salinity increments. Although this does not contradict the reported salinity range for Membras (Martin and Drewry, 1978),

Table 8

Inshore Abundance of *Menidia menidia* and *Membras martinica* in beach seine collections by salinity

		1980			1981		
	PPT	Total catch	Number of hauls	CPUE	Total catch	Number of hauls	CPUE
Membras	0.0-3.9	177	84	2.11	106	112	.95
	4.0-7.9	3	20	.2	14	28	.50
	8.0-11.9	6	14	.4	7	22	.3
	12.0-15.9	5	28	.2	-	10	-
	16.0-19.1	-	18	-	19	20	.95
	20.0-23.9	-	10	-	2	10	.2
Menidia	0.0-3.9	59	84	.70	633	112	5.65
	4.0-7.9	177	20	8.85	507	28	18.1
	8.0-11.9	877	14	62.6	484	22	22.0
	12.0-15.9	1516	28	54.14	735	10	73.5
	16.0-19.1	1123	18	62.39	1742	20	87.1
	20.0-23.9	153	10	15.3	1088	10	108.8

they were expected to be more frequently found in higher salinities (Hildebrand and Schroeder, 1928).

Menidia and Membras were differentially distributed with respect to river drainage system (table 9). For Membras 97% of the total CPUE during 1980 and 76% of the total CPUE in 1981 was in the James River drainage. Conversely, catches of Menidia were lowest in the James River drainage in 1980 (15% of the total CPUE) and 1981 (14% of the total CPUE).

Table 9

Inshore Abundance of *Menidia menidia* and *Membras martinica* in beach seine collections by Drainage and Month

		1980			1981		
	Drainage	Total catch	Number of hauls	CPUE	Total catch	Number of hauls	CPUE
	James	188	67	2.81	123	78	1.6
Membras	York	1	75	.01	5	86	.06
	Rappahannock	2	35	.06	20	46	.43
	James	736	67	10.9	874	78	11.21
Menidia	York	2130	75	28.40	2472	86	28.74
	Rappahannock	1133	35	32.37	1868	46	40.61
	Month						
	July	2	46	.04	96	56	1.7
	August	13	52	.25	8	22	.6
Membras	September	145	49	2.96	14	62	.23
	October	31	30	1.0	30	46	.65
	November	-	-	-	-	24	-
	July	1693	46	36.80	1260	56	22.50
	August	948	52	18.2	1848	22	84.00
Menidia	September	1046	49	21.35	1010	62	16.29
	October	312	30	10.4	799	46	17.4
	November	-	-	-	297	24	12.4

DISCUSSION

The present study has shown that Membras martinica and Menidia menidia are ecologically very different. The feeding experiments and gut content analyses indicate that their feeding strategies are not alike with respect to pelagic and epibenthic feeding. These results were closely corroborated by observed vertical distribution of these species in the lab and field. Obviously, zooplankton prey selection would be an advantageous behavioral adaption for a surface dwelling species (Membras) and the use of epibenthic prey is well suited to the demersal habits of Menidia. This is likely an adaption to life in shallow inshore areas, where large predators occur less frequently and zooplankton would be scarce.

Juveniles of both species probably do not compete interspecifically for resources. Membras spawn inshore in early spring (Hildebrand and Schroeder, 1928; Martin and Drewry, 1978; Polgar et al., 1979). However, the presence of small juveniles in the open waters of the lower Chesapeake Bay has not been reported by previous authors. Adams (1976) stated that the erratic fluctuations in densities of juveniles in eelgrass beds near Beaufort, North Carolina probably suggested Membras did not use eelgrass as a nursery area. If so, then Membras juveniles must move offshore shortly after hatching to open water nursery areas. If the open bay is the major

nursery area for Membras, then the juvenile populations of these two species must be parapatric. Hence, the interspecific competition for resources between Menidia and Membras juveniles (but not necessarily with some other species) would be negligible. Whether Membras are transported to open water via tides, or wind driven currents, or by active migration is not known, but it is an interesting topic for further research.

The relationship between diet and ontogeny was most significant in the shift from exclusive predation on zooplanktonic prey by smaller Menidia to inclusion of both epibenthic and zooplanktonic prey in the diet of larger Menidia. In the Chesapeake Bay, epibenthic prey occurred in stomachs of Menidia >90 mm (appendix A, table A-1). However, in experiment 8 Menidia as small as 61 mm preyed on caprellid amphipods, although higher selection values were calculated from fishes >78 mm. Gilmurray and Daborn (1981) noted this dietary change occurred in Atlantic silversides >81 mm and added that silversides >44 mm fed primarily on Eurytemora hermani, but also ate cumacean shrimp, isopods, amphipods and harpacticoids. The exact size in which the dietary shift occurs in Menidia is therefore quite variable.

Regression analyses of the selection indices for Acartia tonsa adults versus fish length showed significantly positive slopes for both Menidia and Membras. Predation upon A. tonsa copepodites by Menidia was inversely related to fish length and strongest for smaller fishes. I found a significant relationship between fish length and selection of A. tonsa copepodites by Membras in the 32-96 mm size

range. Selection values for caprellid amphipods plotted against Menidia length resulted in a signficantly positive slope (experiment 8, figure 9). Slopes of the regressions for all the remaining prey species in experiments 7 and 8 were not significantly different from 0.

Gilmurry and Daborn (1981) found that 20-40 mm juvenile Atlantic silversides fed exclusively on Eurytemora hermani, though Acartia tonsa was the dominant prey species in their samples of the zooplankton community. They did not know whether the selection of E. hermani over A. tonsa was a function of prey avoidance or prey selection. In the present study, Menidia 30-45 mm taken from nature had eaten Acartia spp. (appendix A, table A-1). Furthermore, all Menidia in the feeding experiments utilized A. tonsa to some degree and most experiments resulted in a positive selection index for A. tonsa. In experiment 8 (figure 8), Menidia as small as 50 mm preyed on adult and copepodite A. tonsa. The implication is that E. hermani was the preferred prey in Gilmurray's study area even with large numbers of A. tonsa available, but in the Chesapeake Bay A. tonsa is abundant and a readily accepted prey for Menidia.

Gilmurray and Daborn (1981) also noted amphipods, isopods, and other benthic organisms as important components in the diet of larger Menidia in the Minas Basin, Bay of Fundy. However, they postulated that strong currents indigenous to the Minas Basin resuspended the benthic organisms, thus making them available to Menidia (Minas Basin has a tidal amplitude of 5-16 meters). Strong currents, especially in

shallow inshore zones are not as intense in the Chesapeake relative to the Minas Basin, yet epifaunal species were captured by Chesapeake Menidia populations (appendix A, table A-1). Although, wind and wave action could resuspend epibenthic prey in the Chesapeake the feeding experiments of the present study were done under static conditions, where Menidia were shown to successfully capture epifaunal prey directly from the bottom.

Membras consistently selected barnacle nauplii rather than copepod nauplii (table 10) even though copepod nauplii were much more abundant than barnacle nauplii throughout the feeding experiments and both were approximately equal in size. Selection indices for barnacle nauplii in the case of Menidia were not consistent among experiments, negative in one experiment, zero in another and significantly positive in a third case. In the selection of barnacle nauplii Membras must be orienting to some unknown prey cue such as shape, or motion. One possible explanation of the selection may lie in barnacle nauplii morphology. A barnacle nauplius possesses two relatively long frontal horns and an elongated posterior spine which may effectively increase their retention on gill rakers of atherinids. Copepod nauplii have no protruding spines or horns, and thus may simply slip through the gill rakers. Atherinids are sight feeders which capture prey by sucking. The interstitial distance between gill rakers must be important in retaining prey when water is driven out of the buccal cavity.

The feeding experiments herein reported do adequately describe the major dietary differences between Menidia and Membras. Feeding

Table 10

Selection Indices for Copepod and Barnacle Nauplii by Feeding Experiment
(see text for symbols definitions)

			Membras				Menidia		
	prey species	P_i	r_i	L_i	N_{stm}	N_{fish}	r_i	L_i	N_{stm}	N_{fish}
EX. 1	copepod nauplii	.457	.257	-.200	159	6	.015	-.442	10	5
	barnacle nauplii	<.001	.079	.079	49		.000	.000	0	
EX. 2	copepod nauplii	.685	.061	-.624	138	5	.009	-.676	3	6
	barnacle nauplii	.037	.463	.426	1039		.015	-.022	5	
EX. 3	copepod nauplii	.817	.018	-.799	41	6				
	banacle nauplii	.009	.081	.072	186					
EX. 4	copepod nauplii	.610	.019	-.589	56	6				
	barnacle nauplii	.023	.076	.053	227					
EX. 6	copepod nauplii	.364					.020	-.344	51	6
	barnacle nauplii	.021					.129	.108	328	

N_{stm} = pooled number of prey in guts.
N_{fish} = number of fishes used in experiment.

experiments in the present study had some design limitations, specifically in terms of the variation in prey species composition from experiment to experiment. Since the dominance and specific proportions of prey species collected from the field changed from day to day and from week to week, the proportions of each prey species were not absolutely consistent for all experiments and undoubtedly contributed to the variation in the observed selection of zooplankton. However, the design is superior to analysis of concomitant samples of predator and prey species taken from the field (see introduction).

The populations of Menidia and Membras are generally parapatric; they inhabit two very different environments (offshore for Membras, inshore for Menidia). Hence, there seems to be little competition and niche overlap between these species. Since their diets and vertical distributions are dissimilar, minimal competitive interaction is expected when the two species overlap. Reid (1954) reported Membras martinica as common along sandy beaches and in open water near the surface with highest abundance in summer months. The present study has shown Membras to be mostly an open water species and rarely found inshore. The presence of 5-19 mm juveniles through August 1981 supports the view of Hildebrand and Schroeder (1928) and Bayliff (1950) that spawning in Membras is protracted.

The cause of the unequal distributions between drainages is not known. Possible explanations in the case of Membras may involve the circulation patterns near the bay mouth which could favor their entrainment into the James compared with the York or Rappahannock

Rivers. Alternatively, the nearness of the James River to the mouth of Chesapeake Bay and areas of higher salinities where Membras are more abundant could be a factor. The observed differences could partially be a function of the fixed station sample design of the inshore striped bass surveys. If the microhabitats sampled were unique to the James River and highly preferred by Membras then consecutive sampling at those stations could produce these results. However, beach seining can only be accomplished in particular types of habitats, such as open beaches with sandy bottoms and no large rocks or other obstructions. Generally, all the stations within each salinity or river mile stratum were quite similar among rivers.

On the surface in daylight several miles from shore, numerous schools of what appeared to be atherinids have been observed. The fishes moved quickly, made frequent turns, and thrashed the water surface. Unfortunately, efforts to sample these schools were unsuccessful, but observations were made close enough to the schools to be certain that they were atherinids. Since Menidia menidia never occurred in open water collections from the lower Chesapeake Bay, it was assumed that they were Membras. The implications are that Membras disperse horizontally at night, and regroup in large schools in daylight, probably for protection against predation. The repeated occurrence of juvenile fishes from 5-19 mm in day and night collections suggests that this schooling behavior is not well developed in smaller individuals.

In numerous daytime beach seine collections, Menidia have always been noted to be in schools at or near the bottom. When Menidia and Membras were together in beach seine catches, it was observed that as the net was brought ashore Membras were gilled in the upper portion of the net while Menidia were trapped at the bottom near the lead line. This differential preference in position in the water column may well explain the observed use of epibenthic prey by adult Menidia, and the exclusive use of zooplankton by Membras. Menidia would thus encounter food resources when inhabiting shallow inshore zones where they are found in great abundance. Similarly, an open water surface dwelling species such as Membras would encounter pelagic zooplankton, and would typically not come in contact with epifaunal communities.

There is considerable confusion in the literature on the overwintering areas of Menidia, and virtually no information on the winter habitats of Membras. Gunter (1945) reported that Menidia leave the bay for offshore areas as water temperature decreased, in direct contradiction to reports that Menidia remain in the bay year round in deep water (Bayliff 1950, Richards and Castagna 1970). Otter trawls in the York river channel taken during the winter months of 1980 and 1981 have captured large Menidia >100 mm (personal observation). However, recent winter occurrences of Menidia in the ocean 170 km offshore from the mouth of the Chesapeake have been observed (Conover and Murawski, in press). It may be likely that only a portion of the population leaves the bay while the others remain in deep channels to overwinter.

The diel movements of Menidia adults and juveniles in nature have not been fully elucidated by the present study. Although Conover and Murawski (in press) observed that Menidia adults move upward off the bottom at night, their study was restricted to offshore oceanic overwintering habitats. At present, no field data exist on the diel movement of Menidia adults and juveniles in shallow inshore habitats. In regard to the day/night schooling behavior of Membras in the open bay, it must be confirmed that the schools found on the surface during daylight are indeed Membras. Also, the mechanism and timing of the offshore migration of Membras juveniles to the center of the bay is not known. Furthermore, the greater abundance of Membras in the James drainage than in the York and Rappahannock drainage is at present an enigma, as are the lower catches for Menidia in the James drainage.

Competition for food and spatial resources between Menidia menidia and its confamilial Membras martinica is minimal. Their respective food and habitat preferences have reduced competitive interactions and interspecific interferences for all life stages. Resource partitioning such as this is undoubtedly beneficial to both, ultimately enhancing each species survival.

Summary of Significant Findings

Feeding Experiments

Adults in Sympatry and Allopatry

1. *Membras* adults utilized zooplankton in their diet almost exclusively regardless of *Menidia* presence or absence.

2. *Menidia* adults utilized both zooplankton and epifaunal organisms in their diet.

3. Selection within the zooplankton assemblage appeared to be generalized and overlapping for *Menidia* and *Membras*.

4. Barnacle nauplii are preferred over copepod nauplii by *Membras* adults and to some extent *Menidia* adults, despite the size similarity between these prey species. The fishes must be orienting to some behavioral or structural cue in their their predation of barnacle nauplii.

Summary of Significant Findings

Feeding Experiments

Ontogentic Changes in Diet

1. Larger Menidia individuals (>65 mm) incorporate epifaunal prey in their diet along with zooplankton.

2. As length increased in Menidia, the selection for A. tonsa adults increased. Conversely, as fish length increased, dependence on smaller A. tonsa copepodites decreased.

3. As length increased in Membras, the selection for A. tonsa adults increased. A trend of decreasing selection of A. tonsa copepodites by larger Membras was evident, but not statistically significant.

4. Copepod nauplii were not important prey for the size range of Menidia studied. It is not known whether Menidia less than 50 mm utilize copepod nauplii in their diet.

5. Copepod nauplii were not an important prey in the diets of Membras between 32-96 mm.

Summary of Significant Findings

Vertical and Geographic Distributions

1. Adult *Membras* and *Menidia* are vertically separated; *Membras* are surface dwellers and *Menidia* orient near the bottom.

2. *Membras* disperse on the surface at night and form large schools at the surface by day; juveniles do not exhibit this behavior.

3. The vast majority of *Membras* populations concentrate in the open waters of the Chesapeake Bay.

4. The open bay appears to be an important nursery area for juvenile *Membras* >5 mm SL.

5. *Menidia* were not taken in open water away from inshore habitats.

6. *Menidia* populations concentrate inshore and upriver in salinities from 4.0 to 24.0 PPT.

7. *Membras* inhabiting inshore zones are much less abundant than *Menidia*.

8. *Membras* is found more frequently in the James River drainage then in either the York or Rappahannock River drainages.

APPENDIX A. Preliminary field observations on diets of *Menidia* and *Membras*.

PRELIMINARY FIELD OBSERVATIONS ON DIET

On July 12, 1980 (2000 hours EDT) a large collection of Menidia menidia and Membras martinica was made in a single seine sweep with a 90' x 4' beach seine at Ware Neck Point on the Ware River, VA. Of the 272 silversides removed from the collection, 180 of them were Menidia menidia and 92 were Membras martinica. All were fixed in formalin and taken to the laboratory for gut content analysis. Each species sample was sorted into 5 mm (total length) sized classes. Gut contents of individual fish were rinsed out with a 5% solution of formalin and pooled for each species into small jars. Each pooled sample was then placed on a gridded petri dish, and examined with an Olympus dark field dissecting microscope for enumeration and identification of prey items. All of the Membras specimens from 69-119 mm and all of the Menidia specimens from 30 mm to 64 mm were analyzed. Of the 146 Menidia collected within the 90 mm to 129 mm size range, 56 individuals were dissected (38% of the total catch within that size range).

Food preference of the Ware Neck specimens was determined by classifying the food items (appendix A, table A-1) into zooplanktonic or benthic/epibenthic groups. A crude measurement of pelagic and epibenthic oriented feeding was obtained by calculating the percent of each category. Excluded from this analysis were nematodes and cilates, because their undigested state indicated that they were stomach parasites. Also excluded were other incidentals such as unidentified trochophores, terrestrial insect parts, fragments of

Table A-1. Results of the stomach content analysis for the *Membras* specimens from Ware Neck Point, VA. Data are numbers of each prey species found in the pooled stomachs of each size class (5 mm increments).

SIZE RANGE MIDPOINT	72.5	82.5	87.5	92.5	97.5	102.5	107.5	112.5	117.5
N	6	4	14	17	21	19	2	3	5
PREY SPECIES									
cladoceran	-	1	-	1	-	-	-	-	-
ostracod	3	6	10	2	53	24	-	1	1
barnacle nauplii	1	2	1	-	-	1	-	-	-
copepod nauplii	-	-	-	-	-	-	-	-	-
Acartia spp.	12	3	4	109	251	639	-	-	-
Oithona sp.	-	-	-	-	-	-	-	-	-
cyclopoid copepod	-	-	-	3	4	5	-	-	1
Saphirella sp.	-	-	1	-	2	5	-	-	1
harpacticoid	11	1	5	1	3	1	-	6	1
amphipod	-	-	-	-	-	-	-	-	-
isopod	-	-	-	-	-	-	-	-	-
Neohaustorius schmitzi	-	-	-	-	-	-	-	-	-
Gammarus mucronatus	-	-	-	-	-	-	-	-	-
polychaete larvae	-	-	-	-	-	-	-	-	-
nemertean (sections) ?	-	-	-	-	-	-	-	-	-
trochophore	-	-	1	-	-	-	-	-	-
nematode (parasite)	5	18	7	4	11	21	-	8	22
ciliate (parasite)	4	1	6	-	5	2	-	1	2
fish eggs	-	-	2	-	29	1	-	1	4
bivalve larvae	-	1	1	-	1	-	-	-	-
terrestrial insect parts	11	-	-	-	3	-	-	-	-
juvenile horseshoe crab	-	-	-	-	-	-	-	-	-
mysid shrimp	-	-	-	-	1	-	-	-	-
crustacean parts	-	-	-	-	-	2	-	-	-
filamentous red algae	-	-	-	-	-	-	-	-	-
amphipod parts	-	-	-	-	-	-	-	-	-

Table A-1 (continued). Results of the stomach content analysis for the *Menidia* specimens from Ware Neck Point, VA. Data are numbers of each prey species found in the pooled stomachs of each size class (5 mm increments).

SIZE RANGE MIDPOINT	32.5	37.5	42.5	47.5	57.5	62.5	92.5	97.5	102.5	107.5	112.5	117.5	122.5	127.5
N	6	13	5	1	1	1	2	15	10	4	9	12	3	1
PREY SPECIES														
ostracod	9	8	3	-	10	1	-	-	-	-	-	-	-	-
barnacle nauplii	-	-	-	-	-	-	-	-	-	-	-	-	-	-
copepod nauplii	2	11	3	-	1	-	-	-	-	-	-	-	-	-
Acartia spp.	7	18	58	-	-	-	-	2	-	-	-	-	-	-
Oithona sp.	-	2	-	-	-	-	-	-	-	-	-	-	-	-
cyclopoid copepod	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Centropages sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-
harpacticoid	42	19	2	2	-	-	-	-	-	-	6	1	-	-
amphipod	-	-	-	-	-	-	-	-	-	-	9	5	-	-
isopod	-	-	1	-	-	-	-	-	1	-	4	1	-	-
Neohaustorius schmitzi	-	3	-	-	-	-	6	21	8	3	-	-	-	-
Gammarus mucronatus	-	-	-	-	-	-	-	3	1	-	-	-	-	-
polychaete larvae	1	-	-	-	-	-	-	-	-	-	-	-	-	-
nemertean (sections) ?	-	-	-	-	-	-	4	26	63	20	115	135	50	9
trochophore	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nematode (parasite)	6	15	1	-	-	-	-	-	-	-	-	-	-	-
ciliate (parasite)	1	2	-	-	6	136	2	75	22	90	159	8	31	31
fish eggs	-	1	-	-	-	-	3	-	4	3	4	17	1	-
bivalve larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-
terrestrial insect parts	-	-	1	-	-	-	-	-	-	-	2	-	-	3
juvenile horseshoe crab	-	-	-	-	-	-	-	1	-	-	-	-	-	-
mysid shrimp	-	-	-	-	-	-	-	-	-	-	-	-	-	-
crustacean parts	-	-	-	-	-	-	-	-	1	-	1	2	-	2
filamentous red algae	-	-	-	-	-	-	-	-	-	-	-	-	-	-
amphipod parts	-	-	-	-	-	-	-	8	-	-	7	-	-	-

copepods and amphipods, and filamentous red algae. Data from stomachs of Membras between 65 to 119 mm were pooled, as were the Menidia from 90 to 129 mm and the 30 to 64 mm (appendix A, table A-2).

Menidia menidia in the 90-129 mm group apparently utilized benthic/epibenthic organisms, while Membras martinica seemed to have been feeding of pelagic prey. Smaller Menidia contained 50% pelagic prey, and 50% epifaunal prey (93% of which were harpacticoids). Stomach contents from 90-129 mm Menidia were dominated by wormlike sections (possible nemerteans), and amphipods. Subsequent collections and gut content analysis of Menidia from various locations around Virginia have shown that fishes of this size also fed on zooplankton such as Acartia tonsa. Based on the above data it was decided to evaluate these apparent feeding relationships under controlled laboratory conditions.

Table A-2. Percent composition of pelagic and epibenthic prey items from Ware Neck collection (based on total numbers of prey).

Membras martinica		
n = 92	size range	65 mm-119 mm
%	Planktonic	84%
%	Benthic	16% (100% were harpacticoids)
Menidia menidia		
n = 27	size range	30 mm-64 mm
%	Planktonic	50%
%	Benthic	50% (93% were harpacticoids)
n = 56	size range	90 mm-129 mm
%	Planktonic	0.1%
%	Benthic	99.9%

APPENDIX B. Raw data from experiments 7 and 8. Pi, proportion of species i in feeding chamber; N, number of prey counted from each individual fish; r_i, ration proportion; L_i, linear selection index.

EXPERIMENT 7 - *Membras martinica*

FL:		96*			84**			84		
Resource	p_i	N	r_i	L_i	N	r_i	L_i	N	r_i	L_i
Acartia tonsa (adults)	.057	230	.753	.695	55	.095	.057	33	.660	.603
A. tonsa (copeps.)	.143	17	.056	-.087	115	.199	.056	5	.100	-.043
Oithona sp.	.055	35	.114	.059	228	.395	.340	3	.060	.005
Paracalanus sp.	.010	2	.007	-.003	11	.019	.009	2	.040	.030
copepod nauplii	.701	7	.023	-.678	160	.277	-.424	3	.060	-.641
barnacle nauplii	.004	4	.013	.009	3	.005	.001	2	.040	.036
Saphirella sp.	.024	1	.003	-.021	2	.004	-.020	0	.000	-.024
other (zooplank.)	.004	8	.026	.022	4	.007	.003	2	.040	.036
harpacticoid	.002	2	.007	.005	0	.000	-.002	0	.000	-.002

* stomach contents diluted to 80 mls; three 10 ml subsamples counted
** stomach contents diluted to 80 mls; three 5 ml subsamples counted

EXPERIMENT 7 (Cont.)

FL:		65*			60**			53***		
Resource	p_i	N	r_i	L_i	N	r_i	L_i	N	r_i	L_i
Acartia tonsa (adults)	.057	79	.435	.378	99	.241	.184	35	.097	.040
A. tonsa (copeps.)	.143	16	.088	-.055	60	.146	.003	57	.158	.015
Oithona sp.	.055	66	.364	.309	195	.475	.420	191	.529	.474
Paracalanus sp.	.010	4	.021	.011	11	.027	.017	20	.056	.046
copepod nauplii	.701	10	.055	-.646	34	.083	-.618	44	.122	-.579
barnacle nauplii	.004	3	.017	.013	10	.024	.020	11	.031	.027
Saphirella sp.	.024	3	.017	-.007	1	.002	-.024	0	.000	-.024
other (zooplank.)	.004	1	.005	.001	1	.002	-.004	3	.008	.004
harpacticoid	.002	0	.000	-.002	0	.000	-.002	0	.000	-.002

* stomach contents diluted to 60 mls; three 10 ml subsamples counted
** stomach contents diluted to 80 mls; three 10 ml subsamples counted
*** stomach contents diluted to 80 mls; three 15 ml subsamples counted

EXPERIMENT 7 (Cont.)

FL:		48*			38			37*		
Resource	p_i	N	r_i	L_i	N	r_i	L_i	N	r_i	L_i
Acartia tonsa (adults)	.057	63	.227	.170	6	.113	.056	4	.014	-.043
A. tonsa (copeps.)	.143	56	.201	.058	8	.151	.008	80	.272	.129
Oithona sp.	.055	118	.423	.368	30	.566	.501	112	.380	.325
Paracalanus sp.	.010	11	.040	.030	0	.000	-.010	23	.078	.068
copepod nauplii	.701	17	.061	-.640	7	.132	-.389	74	.252	-.451
barnacle nauplii	.004	4	.014	.010	0	.000	-.004	1	.003	-.001
Saphirella sp.	.024	2	.008	-.016	0	.000	-.024	0	.000	-.024
other (zooplank.)	.004	8	.028	.024	2	.038	.034	0	.000	.004
harpacticoid	.002	0	.000	-.002	0	.000	-.002	0	.000	-.002

* stomach contents diluted to 80 mls; three 10 ml subsamples counted

EXPERIMENT 7 (Concl.)

FL:			32*	
Resource	p_i	N	r_i	L_i
Acartia tonsa (adults)	.057	8	.016	-.041
A. tonsa (copeps.)	.143	126	.244	.101
Oithona sp.	.055	107	.208	.153
Paracalanus sp.	.010	24	.047	.037
copepod nauplii	.701	253	.490	-.211
barnacle nauplii	.004	6	.012	.008
Saphirella sp.	.024	0	.000	-.024
other (zooplank.)	.004	0	.000	-.004
harpacticoid	.002	0	.000	-.002

* stomach contents diluted to 80 mls; three 5 ml subsamples counted

EXPERIMENT 8 - *Menidia menidia*

FL:		85			84			83		
Resource	p_i	N	r_i	L_i	N	r_i	L_i	N	r_i	L_i
Acartia tonsa (adults)	.066	12	.400	.336	44	.595	.529	70	.380	.314
A. tonsa (copeps.)	.192	2	.067	-.125	15	.203	.011	45	.245	.053
Oithona sp.	.012	6	.200	.188	1	.014	.002	8	.043	.031
Paracalanus sp.	.049	2	.067	.018	4	.054	.005	3	.016	-.033
Pseudodiaptomus sp.	.006	0	.000	-.006	0	.000	-.006	0	.000	-.006
copepod nauplii	.515	3	.100	-.415	1	.014	-.501	8	.043	-.472
barnacle nauplii	.036	0	.000	-.036	2	.027	-.009	8	.043	.007
Saphirella sp.	.096	0	.000	-.096	0	.000	-.096	6	.033	-.063
other (zooplank.)	.001	0	.000	-.001	0	.000	-.001	0	.000	-.001
harpacticoid	.009	0	.000	-.009	0	.000	-.009	1	.005	-.004
gammarid amphipod	.014	0	.000	-.014	2	.027	.013	0	.000	-.014
isopod	.001	0	.000	-.001	0	.000	-.001	1	.005	.004
caprellid amphipod	.004	4	.133	.129	5	.068	.064	32	.174	.174
ostracod	.002	1	.003	.031	0	.00	-.002	2	.011	.009

EXPERIMENT 8 (Cont.)

FL:		80			78			70		
Resource	p_i	N	r_i	L_i	N	r_i	L_i	N	r_i	L_i
Acartia tonsa (adults)	.066	192	.444	.378	254	.526	.460	24	.235	.169
A. tonsa (copeps.)	.192	133	.308	.116	121	.251	.059	32	.314	.122
Oithona sp.	.012	17	.039	.027	8	.017	.005	9	.088	.076
Paracalanus sp.	.049	29	.067	.018	13	.027	-.022	8	.078	.029
Pseudodiaptomus sp.	.006	0	.000	-.006	0	.000	-.006	0	.000	-.006
copepod nauplii	.515	8	.019	-.496	9	.019	-.496	7	.069	-.446
barnacle nauplii	.036	9	.021	-.015	19	.039	.003	13	.127	.091
Saphirella sp.	.096	20	.046	-.050	8	.017	-.079	6	.059	-.037
other (zooplank.)	.001	0	.000	-.001	0	.000	-.001	0	.000	-.001
harpacticoid	.009	5	.012	.003	8	.017	.008	2	.020	.011
gammarid amphipod	.014	0	.000	-.014	0	.000	-.014	0	.000	-.014
isopod	.001	0	.000	-.001	0	.000	-.001	0	.000	-.001
caprellid amphipod	.004	16	.037	.033	41	.085	.081	1	.010	.006
ostracod	.002	3	.007	.005	2	.004	.002	0	.000	-.002

EXPERIMENT 8 (Cont.)

FL:		65*			57*			56*		
Resource	p_i	N	r_i	L_i	N	r_i	L_i	N	r_i	L_i
Acartia tonsa (adults)	.066	82	.255	.189	114	.323	.257	130	.267	.201
A. tonsa (copeps.)	.192	163	.508	.316	190	.453	.261	229	.470	.278
Oithona sp.	.012	15	.047	.035	10	.028	.016	19	.039	.027
Paracalanus sp.	.049	13	.040	-.009	14	.040	-.009	28	.057	.008
Pseudodiaptomus sp.	.006	0	.000	-.006	0	.000	-.006	0	.000	-.006
copepod nauplii	.515	18	.056	-.459	29	.082	-.433	32	.066	-.449
barnacle nauplii	.036	23	.072	.036	21	.060	.024	45	.092	.056
Saphirella sp.	.096	2	.007	-.089	4	.011	-.085	3	.006	-.090
other (zooplank.)	.001	0	.000	-.001	0	.000	-.001	0	.000	-.001
harpacticoid	.009	3	.009	.000	1	.003	-.006	1	.002	-.007
gammarid amphipod	.014	0	.000	-.014	0	.000	-.014	0	.000	-.014
isopod	.001	0	.000	-.001	0	.000	-.001	0	.000	-.001
caprellid amphipod	.004	1	.003	-.001	0	.000	-.004	0	.000	-.004
ostracod	.002	1	.003	.001	0	.000	-.002	0	.000	-.002

* ration proportions estimated by dilution of stomach contents to 80 mls; three subsamples (5 mls each) were counted

EXPERIMENT 8 (Cont.)

FL:		52*			51*			51*		
Resource	p_i	N	r_i	L_i	N	r_i	L_i	N	r_i	L_i
Acartia tonsa (adults)	.066	128	.288	.221	134	.312	.246	99	.237	.171
A. tonsa (copeps.)	.192	227	.510	.318	197	.458	.266	247	.591	.399
Oithona sp.	.012	6	.013	-.001	13	.030	.018	13	.031	.019
Paracalanus sp.	.049	21	.047	-.002	20	.047	-.002	13	.031	-.018
Pseudodiaptomus sp.	.006	0	.000	-.006	0	.000	-.006	0	.000	-.006
copepod nauplii	.515	19	.047	-.468	20	.047	-.468	21	.050	-.465
barnacle nauplii	.036	41	.092	.056	39	.091	.055	22	.052	.016
Saphirella sp.	.096	0	.000	-.096	4	.009	-.087	2	.005	-.091
other (zooplank.)	.001	0	.000	-.001	0	.000	-.001	0	.000	-.001
harpacticoid	.009	3	.007	-.002	3	.007	-.002	1	.002	-.007
gammarid amphipod	.014	0	.000	-.014	0	.000	-.014	0	.000	-.014
isopod	.001	0	.000	-.001	0	.000	-.001	0	.000	-.001
caprellid amphipod	.004	0	.000	-.004	0	.000	-.004	0	.000	-.004
ostracod	.002	0	.000	-.02	0	.000	-.002	0	.000	-.002

* ration proportions estimated by dilution of stomach contents to 80 mls; three subsamples (5 mls each) were counted

EXPERIMENT 8 (Cont.)

FL: 51*

Resource	p_i	N	r_i	L_i
Acartia tonsa (adults)	.066	107	.242	.176
A. tonsa (copeps.)	.192	227	.512	.320
Oithona sp.	.012	12	.027	.015
Paracalanus sp.	.049	13	.032	-.017
Pseudodiaptomus sp.	.006	1	.002	-.004
copepod nauplii	.515	35	.079	-.436
barnacle nauplii	.036	39	.088	.056
Saphirella sp.	.096	5	.012	-.084
other (zooplank.)	.001	0	.000	-.001
harpacticoid	.009	3	.007	-.002
gammarid amphipod	.014	0	.000	-.014
isopod	.001	0	.000	-.001
caprellid amphipod	.004	0	.000	-.004
ostracod	.002	0	.000	-.002

* ration proportions estimated by dilution of stomach contents to 80 mls; three subsamples (5 mls each) were counted

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